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ENERGY FLOW THROUGH FREE-LIVING SOIL NEMATODES IN HIGH ARCTIC TERRESTRIAL COMMUNITIES

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL, 1979

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ENERGY FLOW THROUGH FREE-LIVING SOIL NEMATODES IN HIGH ARCTIC TERRESTRIAL COMMUNITIES, submitted by Dennis Lester Coor Procter in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Entomology.

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ABSTRACT

Several aspects of the ecology of free-living soil nematodes, including their role in energy flow, were studied on the Truelove Lowland high arctic terrestrial ecosystem. The study included a broad field investigation of the nematode fauna as a whole, and a detailed laboratory investigation of the respiratory physiology, growth, and population growth of a single species, *Chiloplacus* sp.

The respiratory physiology of some other important arctic invertebrates was also studied.

The study was conducted in four habitats, which formed a continuum from the crest of a raised beach to a low-lying meadow in terms of change in topography and microclimate. These habitats were equated with different major communities characteristic of the low and high arctic.

Nematode densities and biomass were measured in the four habitats, and production was estimated for two of these habitats. Densities and biomass increased progressively from crest, through slope, to transition, and reflected increasing vegetation from crest to transition. The meadow had the most vegetation but fewest nematodes, and appeared to be a relatively unfavorable nematode habitat because of its wetness and low temperatures.

The nematodes were concentrated in the top 5 cm of soil, where organic matter was greatest and temperatures were highest.

Nematode production varied markedly with season, habitat, and soil depth. Differences in climate and microclimate, and particularly temperature, appeared to govern production.

Nematodes dominated invertebrate production in the drier habitats, probably because of their anhydrobiotic and cryptobiotic capabilities. They were less important in the wettest areas because of cold temperatures, limited oxygen, and restricted mobility.

Compared with their role in other ecosystems, nematodes are a relatively important part of this high arctic ecosystem. Furthermore, they are important in most arctic communities. Above average tolerance of the conditions in this ecosystem, and their general flexibility as relatively r selected organisms, probably accounts for their importance in high arctic communities.

The oxygen consumption of other common terrestrial and aquatic invertebrates from the Truelove Lowland was similar to published information for arctic, antarctic, and alpine invertebrates at the same temperatures. When species were compared, metabolic rate was directly proportional to weight, but when different developmental stages were compared, metabolic rate usually increased more slowly than weight.

Values of Q_{10} varied between 1.19 and 9.20, with a 4.01 mean, for the 2°-12°C temperature interval.

The mean Q_{10} values were close to the equivalent values on Krogh's standard metabolic curve but, because of several very large values, most of the specific values obtained were lower than predicted by Krogh's curve. The smallest Q_{10} values occurred in both terrestrial and aquatic species.

While there is evidence of adaptation of metabolic rate to cold, thermoregulatory behaviour, including the ability to select favorable microclimates, is probably the predominant 'arctic' adaptation to cold.

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Chapter 1

THESIS OBJECTIVES AND STUDY SITE

1.1 Introduction

Nematodes are among the most ubiquitous and abundant of all invertebrates, occupying a wide range of niches in almost every environment. They often hold an important position in ecosystems by feeding on the primary producers, the algae and higher plants. Many others are predators and parasites of animals. However, in terms of trophic levels, the major role of nematodes appears to be at the second level, mainly by feeding on bacteria and fungi, the primary decomposers of organic matter. This is particularly true of soil environments, where the free-living microbivorous nematodes are usually much more abundant than herbivorous, predatory and parasitic nematodes.

The distribution of free-living soil nematodes in particular bears little relationship to major geographical features such as mountain ranges, ocean barriers, and climatic zones. To a striking degree, genera and species occur in all parts of the world, and in a variety of habitats encompassing a wide range of soils, climates, and vegetation. For example, Plectus cirratus has been collected from soil in Denmark, moss high in the Pamirs, and the Baltic Sea (Nicholas, 1975). Nielsen (1949), in a landmark study of the fauna of Danish soils, found that most species were eurytopic (occupy diverse habitats) reinforcing, on a smaller scale, the generalization made on cosmopolitan distributions. Later workers, including Wasilewska (1970) and Domurat (1970), have confirmed the high frequency of eurytopic species in other faunas.

The wide distribution of many species, and the apparently diverse habitats individual species occupy, may reflect their long evolutionary history. Even more important may be their striking tolerance of abiotic environmental factors. Tolerance of oxygen shortage, freezing, and wide range of temperature and salinity is common (Nicholas, 1975; Wallace, 1971). Many species survive desiccation, and can be dispersed in a crytobiotic state. However, despite the evident versatility of free-living soil nematodes, there is little knowledge of the factors which determine the detailed composition of faunas, making it difficult to explain the overlap between faunas of different habitats.

The almost universal abundance of free-living nematode species extends to arctic habitats, as exemplified by species lists for both the Low Arctic (Cobb, 1921; Kuzmin, 1973) and High Arctic (Mulvey, 1963). Until recently, the only information available on free-living nematodes of arctic habitats was faunal lists. In the past decade several arctic and antarctic ecosystem studies conducted within the International Biological Programme Tundra Biome series of co-operative projects have extended our knowledge of the role of nematodes, primarily by providing estimates of densities, biomass, and classification of species on the basis of trophic role (e.g. Spaull, 1973; MacLean, 1974; Procter, 1977a). However, these estimates of energy flow are preliminary, because some required information, such as repiration rates, was calculated from data obtained under conditions unrepresentative of the arctic (e.g. high temperature), using extrapolation methods, such as Krogh's temperature-metabolism curve (cf. Lagerlöf, Magnusson and Rosswall, 1975), that appear inappropriate (Procter, 1977b).

In my study I investigated the role of free-living soil nematodes in energy flow through a High Arctic terrestrial ecosystem. This information presented in this thesis extends and refines recently published estimates of nematode seasonal standing crop, respiration and production (Procter, 1977a) by utilizing detailed information on physiology and development at low temperatures that is lacking in both my publication and in other studies of arctic nematodes.

The study was carried out on the Truelove Lowland (76° 33' N, 84° 40' W), Devon Island, Canada (Fig. 1), and constituted one part of the Devon Island project, which was a comprehensive integrated study of a High Arctic terrestrial ecosystem. The Devon Island project was part of the Canadian contribution to the International Biological Programme, and was one of 14 major ecosystem studies conducted with the I.B.P. Tundra Biome. Within this group of projects it was the only one of four major arctic studies that was conducted within the High Arctic (Rosswall and Heal, 1975).

1.2 Site Description

Bliss (1977a) described the physiography of the Truelove Lowland and surrounding area. Krupicka (1977) and King (1969) may be consulted for more detail on local geology and the periglacial features of the area.

The outstanding topographical feature of the Truelove Lowland is a series of fossil raised beach ridges, which occur as more than 20 successive steps across the Lowland (Fig. 1). Barr (1971) discussed the origin of the Lowland beaches in terms of post-glacial isostatic rebound. Andrews (1970) has considered post-glacial rebound in the wider context of the Canadian Arctic.

A series of lakes and meadows alternate with the raised beaches across the Lowland. The lakes were formed from lagoons cut off during uplift by the offshore bars which formed the raised beaches across the Lowland. Some of these lakes filled in with lacustrine deposits to form meadows. Typically lakes, or wet sedge-moss meadows, occur upslope of the ridges, while better drained sedge areas occur downslope (Bliss, 1977a).

1.3 Habitat Descriptions

Seven major topographic-plant communities, with several subdivisions, were recognized on the Truelove Lowland (Muc and Bliss, 1977). The Devon Island Project studied two communities intensively : the hummocky sedge-moss meadow, and the raised beach complex (Fig. 2). Bliss (1977a) provides maps locating the two sets of studies.

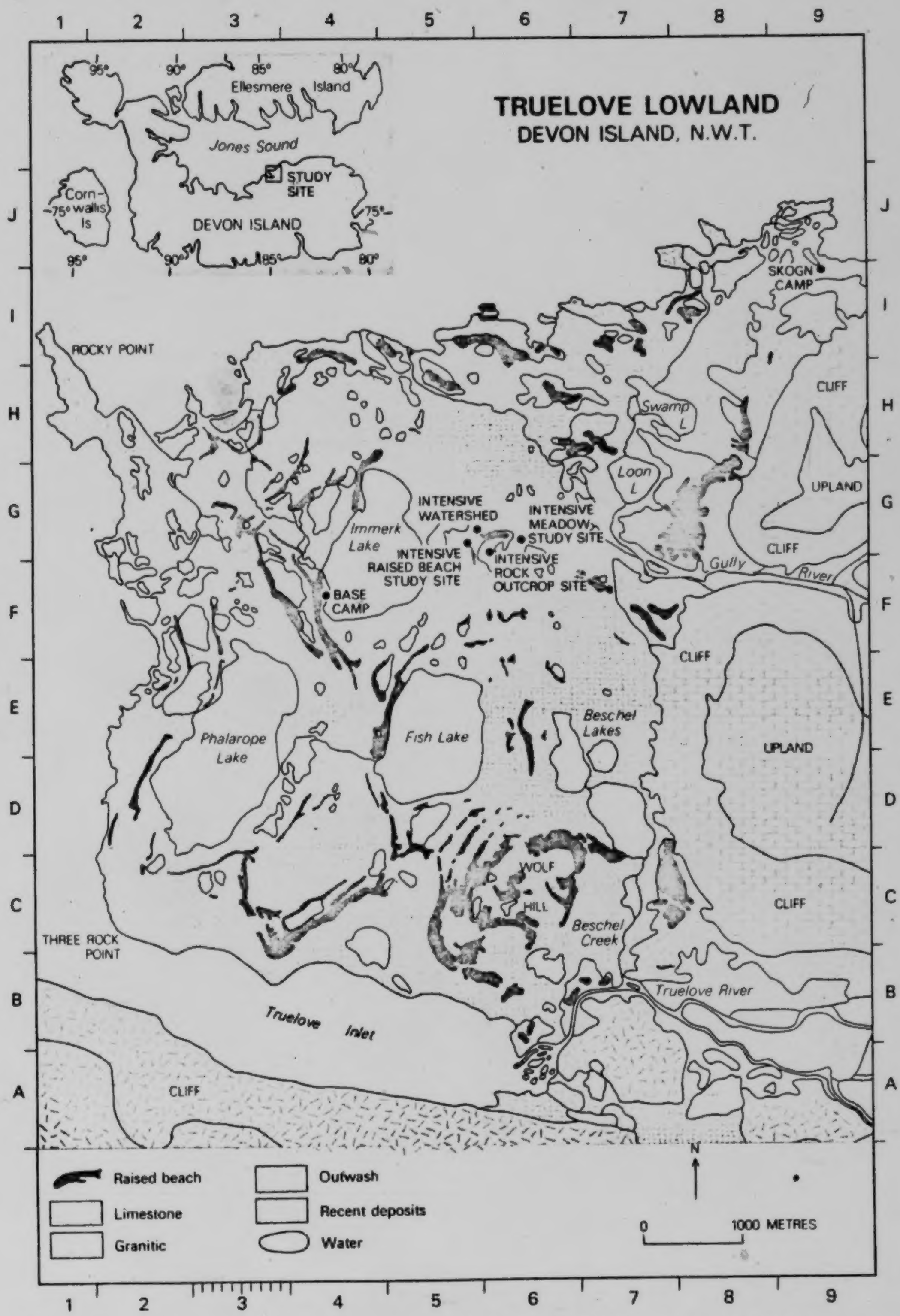

TRUELOVE LOWLAND
DEVON ISLAND, N.W.T.
95°
90°
85°
80°
Ellesmere Island
Jones Sound
STUDY SITE
Corn-wallis Is
75°
DEVON ISLAND
ROCKY POINT
SKOGN CAMP
CLIFF
Swamp L
Loon L
UPLAND
Immerk Lake
INTENSIVE WATERSHED
INTENSIVE MEADOW STUDY SITE
INTENSIVE RAISED BEACH STUDY SITE
INTENSIVE ROCK OUTCROP SITE
Gully River
BASE CAMP
Phalarope Lake
Fish Lake
Beschel Lakes
WOLF HILL
Beschel Creek
THREE ROCK POINT
Truelove River
Truelove Inlet
N
Raised beach
Limestone
Granitic
Outwash
Recent deposits
Water
0
1000 METRES
1 2 3 4 5 6 7 8 9
A B C D E F G H I J

Fig. 1. General topography of the Truelove Lowland and location of the intensive study sites (modified from Bliss, 1977a).

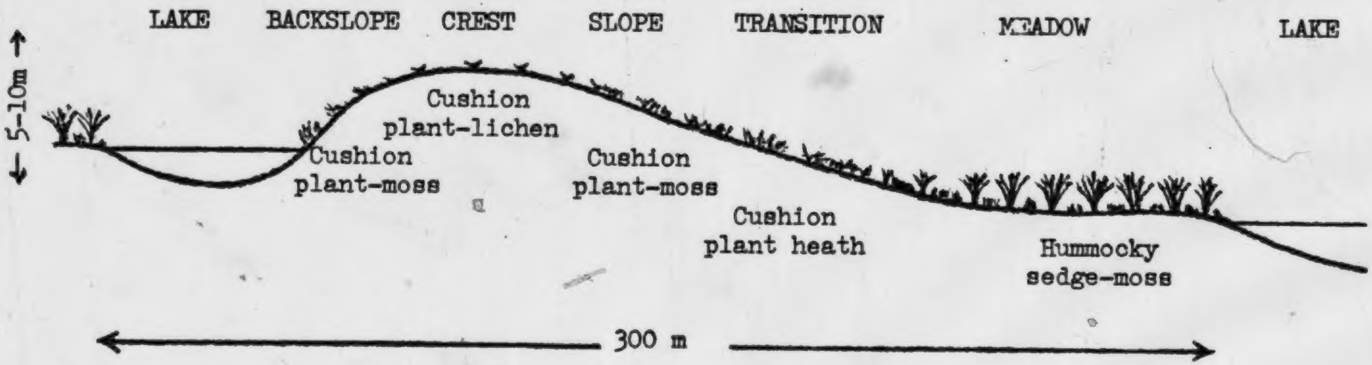

LAKE
BACKSLOPE
CREST
SLOPE
TRANSITION
MEADOW
LAKE
5-10m
Cushion plant-lichen
Cushion plant-moss
Cushion plant-moss
Cushion plant heath
Hummocky sedge-moss
300 m

Fig. 2. The four study habitats (crest, slope, transition and meadow), and the general pattern of plant communities in relation to a raised beach ridge and an adjacent filled-in lake basin (modified from Muc and Bliss, 1977).

1.4 Thesis Objectives

The primary objectives of my study were dictated by the general goals of the Devon Island Project. According to Bliss (1977a) the main objectives of the project were to :

1. determine population numbers and standing crop for the major biological components of the Truelove Lowland and express these data on a land area basis by major habitats (topography - plant community);
2. determine rates of energy flow through the total system and its major habitat subcomponents (sedge-moss meadows, and raised beach systems);
3. determine efficiency of the system in capturing and utilizing energy at different trophic levels;
4. determine the environmental and biological limiting factors for growth and development of important plant and animal species; and
5. develop static and dynamic models of high arctic ecosystem function, and function of its component parts.

In order to accomplish the objectives of the Devon Island Project, I initially established the following research goals, based on complementary approaches involving (1) general field studies of the nematode fauna, (2) detailed laboratory studies of a single 'representative' species, and (3) use of the Ryan and Whitfield invertebrate production model (Ryan, 1977a) to estimate respiration and production. My detailed goals were as follows:

1. multispecies studies;
    - (a) determine nematode faunal composition,
    - (b) estimate nematode densities and standing crop (dry weight and calories) at two soil depths for two seasons in the crest, slope, transition and meadow (Fig. 2), and
    - (c) measure respiration (oxygen consumption) of the species complex from the field at commonly encountered temperatures.
2. single species studies (of *Chiloplacus* sp.*);
    - (a) determine individual growth rate and form of the growth curve at an appropriate temperature,
    - (b) determine reproductive rate at the selected temperature,
    - (c) measure population growth at temperatures encompassing those encountered in the field,
    - (d) measure respiration of all stages, at temperatures encompassing those encountered in the field, and
    - (e) determine temperature below which development does not occur, and establish physiological development time (degree-days).

An important purpose of the general and specific studies was to provide information suitable for use in the Ryan and Whitfield predictive invertebrate production model (Ryan, 1977a), in order to estimate mean seasonal standing crop, generation time, respiration, and production.

To this end, the data and derived functions obtained from the studies were synthesized to describe the performance of an 'average' nematode for each of the habitats investigated (cf. Procter, 1977a).

Although the Ryan and Whitfield production model is a convenient and apparently powerful research tool, it remains unproven. Because my research provided independent estimates of some important parts of the model's output, as part of my research objectives I have undertaken to test some aspects of the model's assumptions and functioning.

I noted in Section 1.1 that at least one study of nematode physiological performance in cold environments used respiration estimates extrapolated by means of Krogh's temperature-metabolism curve from data obtained at high temperatures. This procedure, which has been used in studies of other arctic invertebrates (e.g. Scholander et al., 1953), may be suspect, particularly when investigating the possibility of adapted metabolic curves (cf. Procter, 1977b). In order to better understand the relative performance of invertebrates at low and high temperatures, my single species studies included measurements of repiration and population growth at both arctic and temperate/tropical temperatures.

As I attained the primary objectives of my project, questions of more general interest replaced them, the most important being to :

1. explain the large number of nematode species in arctic ecosystems;

2. account for the generally high nematode densities in arctic ecosytems compared with other ecosystems;
3. explain the high standing crop, respiration and production of arctic nematodes compared with other arctic invertebrates;
4. explain the difference in nematode densities, respiration and production between the different arctic habitats studied, and thereby predict and explain the relative importance of nematodes in diverse communities throughout the arctic; and
5. generalize on what makes a successful arctic invertebrate, drawing initially on my knowledge of arctic nematodes.

Very few invertebrate groups are represented in the Arctic, and only very few of those present are conspicuous by their success, at least in terms of abundance. Nematodes, because they are one of the successful groups, may go a long way to answering the question posed by Downes (1962) - "What is an arctic insect?" The final undertaking of this study is to develop and extend the ideas presented by Downes (1962, 1964, 1965) in his several interesting papers, and broaden our understanding of what makes an arctic invertebrate through the extra dimensions offered by the population/energetics approach I have taken in my study.

Muc (1977) and Svoboda (1977) described the flora of the meadow and raised beach respectively, while other investigators obtained complementary information on abiotic factors, including microclimate (Courtin and Labine, 1977), soil (Walker and Peters, 1977) and permafrost (Brown, 1977).

*I have neither identified nor described Chiloplacus sp. I sent material to Dr. R. H. Mulvey and Dr. R. V. Anderson, and was advised that identification and/or description required a substantial taxonomic study. The characters used to separate species of Chiloplacus have been shown to be much more variable than previously thought, and laboratory studies under a range of physical conditions are required to establish the extent of this variability. Consequently, this genus, and the closely related genus Acrobeloides, are in urgent need of revision (Anderson, pers. comm.). However, I have deposited voucher specimens with the Department of Entomology, University of Alberta.

Chapter 2

THE DIVERSITY OF THE NEMATODE FAUNA OF TRUELOVE LOWLAND AND SIMILAR ARCTIC ENVIRONMENTS

2.1 Introduction and Methods

High latitudes generally support less diverse faunas than do tropical regions (e.g. Dobzhansky, 1950). It is also evident that high altitudes have fewer species than do low altitudes. The reasons why some environments have many kinds of organisms, while others support limited numbers of species, are still unclear. Several theories have been proposed to explain both latitudinal and local patterns in species diversity, all of which probably operate in some situations (Pianka, 1966). Pianka (op.cit.) has reviewed the theories that have been proposed to explain these differences.

A striking feature of the invertebrate faunas of Arctic and Antarctic terrestrial environments is the large contribution made by nematodes to the total number of species present in these faunas (e.g. Mulvey, 1963; Spaull, 1973a; Kuzmin, 1973). The relative diversity of high latitude nematode faunas is emphasized by comparison with the nematode faunas of temperate and tropical environments (e.g. Nielson, 1949; Banage and Visser, 1967; Willard et al., 1973; Wasilewska, 1970; Yeates, 1967, 1970, 1972, 1973) - some lower latitude environments appear to support fewer species.

The purposes of this chapter are to : (1) show that the diversity of free-living soil nematode faunas is high in high latitude environments; (2) explain the diversity of high latitude free-living soil nematode faunas relative to low latitude nematode faunas; and (3) suggest why nematodes often dominate high latitude invertebrate species lists. In order to accomplish these goals I compared my Truelove Lowland data with published information on the composition of soil nematode faunas from a variety of arctic, antarctic termperate and tropical locations. I have undertaken to explain the trends I perceived in these data in terms of the various theories offered in explanation of patterns of species diversity.

2.2 Results

Preliminary studies of the Truelove Lowland fauna produced 18 genera belonging to 11 families and six orders (Table 1). Individuals of the genus Plectus occurred in large numbers in 80% of the samples studied, while the genus Dorylaimus was numerous in half of the samples. Substantially less abundant were Tylenchus and Rhabdolaimus, which were common in 20% of the samples. The remaining genera were common in only 15-10% of the samples.

A more thorough investigation of the fauna of Lake Hazen, Ellesmere Island, which is a somewhat simpler high arctic environment than Truelove Lowland, produced 76 species belonging to 43 genera (Table 2). The genus Plectus was numerically important at Lake Hazen.

Tundra environments in general exhibit a wide range of species/genus diversities - from a low of 10 species/6 genera on the Antarctic continent, to a high of 162 species/ 69 genera in subarctic U.S.S.R. (Table 2). The diversity of the nematode fauna of Antarctic regions is much lower than that of Arctic regions.

In terms of numbers of individuals contributed, the genus Plectus was either dominant or co-dominant in most of these high latitude faunas (Table 2). For example, plectids accounted for 70% of the specimens collected by Cobb (1921) from the Canadian Arctic and Alaska, and contributed five of the 10 species recorded from the Antarctic continent. Two exceptions were the relatively

Table 1. Preliminary list of nematode genera found on Truelove Lowland. Numerically dominant genera, in numbers of individuals present, are marked with an asterisk.

Order	Family	Genus
Monhysterida	Monhysteridae	*Monhystera*
Araeolaimida	Plectides	**Plectus* *Anaplectus* *Rhabdolaimus*
	Axonolaimidae	*Cylindrolaimus*
Teratocephalida	Teratocephalidae	*Teratocephalus*
Rhabditida	Cephalobidae	*Acrobeloides* *Chiloplacus* *Acrobeles*
Tylenchida	Aphelenchoididae	*Aphelenchoides*
	Tylenchidae	*Tylenchus* *Tylenchorhynchus*
	Neotylenchidae	*Neotylenchus*
	Heteroderidae	*Heterodera*
Dorylaimida	Monochidae	*Mononchus* *Prionchulus*
	Dorylaimidae	**Dorylaimus* *Carcharolaimus*

Table 2. The number of nematode genera, species and numerically dominant genera in arctic, antarctic, and alpine environments, and in related cool temperate mires.

Habitat	Genera/ Species	Numerically Dominant Genera	Author
High Arctic Tundra: Lake Hazen, Canada (81° 49'N, 71° 18'W)	43/76	Plectus	Mulvey, 1963, 1969a, 1969b, 1969c; Das 1964; Wu, 1969
Various habitats on the Canadian Arctic and Alaska	22/47	Plectus	Cobb, 1921
Various habitats on Vest Spitzbergen (79° N 12'E)	45/89	Tylenchus, Teratocephalus, Cervidellus, Plectus	Loof, 1971
Subarctic Tundra; Tareya, U.S.S.R.	69/162	Eudorylaimus, Plectus	Kuzmin, 1973
Subalpine Tundra: Stordalen, Sweden (68° 22'N, 19° 3'E)	10+/-	Tylenchida, Plectus, Teratocephalus	Lagerlöf et al. 1975
Moorland: Moor House, England (54° 65'N, 2° 45'W)	38/-	Tylenchus	Banage, 1963

Table 2. Continued

Habitat	Genera/ Species	Numerically Dominant Genera	Author
Peatland: Glenamoy, Ireland (54° 12'N, 9° 45'W)	49/85	*Tylenchus*, *Plectus*, *Anaplectus*, *Rhabdolaimus*	Behan, 1973
Long's Peak (4345 m): Colorado (40° 16'N, 105° 37'W)	10/18	*Tylenchus*, *Dorylaimus*, *Plectus*	Thorne, 1929
Subantarctic Tundra: Macquarie Island (54° 30'S, 158° 57'E)	10/26	*Dorylaimus*, *Rhabditis*, *Monhystera*, *Prismatolaimus*	Bunt, 1954
Antarctic Tundra: Signy Island (60° 43'S, 45° 38'W)	19/30	*Teratocephalus*, *Plectus*	Spaull, 1973
Various habitats on the Antarctic Continent (65°-77° S)	6/10	*Plectus*	Various - In: Timm, 1971

low latitude Moor House and Macquarie Island sites, where Tylenchus and Dorylaimus dominated respectively. These two genera were co-dominant with Plectus at several other sites. Teratocephalus was also important at several locations.

Temperate and tropical habitats also showed a wide range of species diversities (Table 3). A tropical grassland savanna (New Hebrides) has the lowest diversity with 12 species/12 genera, while temperate hardwood forest (U.S.A.) was highest with 95 species. The average diversity of the four tropical habitats listed was lower than the averages of the Arctic and temperate habitats, but was higher than that of the Antarctic region.

Tylenchids, including the genera Tylenchus, Helicotylenchus, Tylenchorhynchus and Ditylenchus, and dorylaimids were among the dominant groups in many of the temperate and tropical habitats (Table 3). On the other hand, apart from several temperate environments (e.g. Heath Moor, Maritime Turf and Beech Forest), plectids contributed insignificant numbers of individuals to most of these faunas.

Table 3. The number of nematode genera, species, and numerically dominant genera in various temperate and tropical environments.

Habitat	Genera/ Species	Numerically Dominant Genera	Author
Natural Grassland: Canada.	26/-	_Tylenchus_, _Helicotylenchus_, _Xiphinema_	Willard _et al_., 1973
Natural Grassland: England	42/76	_Tylenchus_, _Paratylenchus_, _Dorylaimids_, _Alaimus_, _Helicotylenchus_	Yuen, 1966
Grass Field: Denmark	21/33	_Tylenchorhynchus_, _Aphelenchoides_, _Pristmatolaimus_ _Monhystera_	Nielsen, 1949
Heath Moor: Denmark	19/31	_Plectus_, _Dorylaimus_, _Tylenchus_	Nielsen, 1949
Maritime Turf: Orkney Island	18/21	_Eudorylaimus_, _Anaplectus_, _Tripyla_	Yeates, 1970

Table 3. Continued

Habitat	Genera/ Species	Numerically Dominant Genera	Author
Regenerated Woodland: England	38/62	*Tylenchus*, *Alaimus*, *Rhabditids*, *Dorylaimids*	Yuen, 1966
Spruce Forest: Denmark	19/23	*Dorylaimus*, *Acrobeles*, *Cephalobus*	Nielsen, 1949
Beech Forest: Denmark	44+/75+	*Tylenchus*, *Ditylenchus*, *Plectus*	Yeates, 1972
Sand Dune Forest (early succession): Poland	25/35	*Eudorylaimus*, *Ditylenchus*, *Tylenchorhynchus*	Wasilewska, 1970
Sand Dune Forest (late succession): Poland	45/71	*Tylenchus*, *Aphelenchoides*, *Eudorylaimus*, *Plectus*, *Acrobeloides*	Wasilewska, 1970
Hardwood Forest (Sugar Maple): Indiana, U.S.A.	-/95	*Tylenchus*, *Tylenchorhynchus*, *Helicotylenchus*	Johnson *et al.*, 1973

Table 3. Continued

Habitat	Genera/ Species	Numerically Dominant Genera	Author
Hardwood Forest (Black Locust): Indiana, U.S.A.	-/58	*Helicotylenchus*, *Tylenchus*	Johnson *et al*., 1973
Dune Sand (Taylor's Mistake): New Zealand	30/32	*Dolichdorus*, *Acrobeles*, *Aporcelaimellus*	Yeates, 1967
Virgin Bush: Uganda	31+/-	*Helicotylenchus* *Dorylaimids*, *Cephalobus*	Banage and Visser, 1967
Tropical Rain Forest: New Hebrides	23/24	*Tylenchus*, *Mitoaxonchium*, *Falcihasta*	Yeates, 1973
Montane Tropical Rain Forest:	17/19	*Cephalobus*, *Tylencholaimus*	Yeates, 1973
Grassland Savanna: New Hebrides	12/12	*Helicotylenchus*, *Aporcelaimellus*	Yeates, 1973

2.3 Discussion

2.3.1 Faunal Lists

Because the composition of the free-living soil nematode faunas of the major biomes is poorly known - Jenkins and Taylor (1967) believe that 2% of existing species have been described - conclusions regarding the diversity of nematodes in different biomes must be tentative. However, Oostenbrink (1966) stated that "The density and polyvalence of nematode populations are generally lower in subtropical and tropical than in moderate climate". Dao (1970) listed 426 species of plant-parasitic and soil inhabiting nematodes from the Netherlands (temperate deciduous and rain forest biome), but listed only 177 species from Venezuela, which encompasses three tropical biomes (Kormandy, 1969). These figures make interesting comparison with the 162 species collected from a much smaller area of tundra in subarctic U.S.S.R. (Kuzmin, 1973). Though clearly incomplete, the information I have presented shows the diversity of nematode faunas of habitats within tropical biomes can be lower than that of habitats in characteristically mid- and high latitude biomes.

While soil living nematodes maintain high species diversity far into high latitudes, particularly to the north, the composition of the fauna changes with latitude. Mulvey (1963) noted that the bacteria-feeding genus Rhabditis, which is common south of the Arctic Circle, is absent from collections made in Alaska and Canada north of the Arctic Circle. More interesting, however, is the change in importance of nematodes parasitizing flowering plants relative to lower plant- (i.e. mosses, lichens, algae, fungi) and bacteria-feeding nematodes with latitude. Mulvey (op. cit.) recorded only two species of confirmed higher plant parasites from High Arctic Lake Hazen - Aguina agrostis, which parasitized the seed heads of Arctagrostis latifolia, and a species of Ditylenchus, which attacked the leaves of Dryas integrifolia. Mulvey listed another eight genera as suspected plant parasites, but at least five of these genera may feed on lower plants (cf. Goodey and Goodey, 1963).

Lagerlöf et al. (1975) reviewed the occurrence of nematode taxa and feeding groups for several high latitude habitats, including some of the tundra sites listed in Table 2. Microbe -feeding nematodes dominated most of the faunas, including those of Stordalen, Signy Island, Macquarie Island and Tareya tundra sites. Microbe-feeding nematodes also dominated the Truelove Lowland fauna (this study), and the fauna of northern Alaska and Arctic Canada in general (Cobb, 1921; Mulvey, 1963). Species of the genera Plectus and Teratocephalus feed on bacteria, while Dorylaimus and Eudorylaimus feed on a variety of micro-organisms. Plant-feeding nematodes dominated the fauna of the more temperate Moor House (Banage, 1963). However, this observation requires qualification because the dominant genus Tylenchus includes facultative and obligate lower-plant feeding species (Wood, 1973; Andrássy, 1976). Tylenchids were co-dominant at Glenamoy, which is a cool temperate mire similar to Moor House (Behan, 1973).

Loof (1971) compared the fauna of Spitzbergen with that of temperate Europe and found that several genera of confirmed higher-plant parasites commonly found in Europe were absent from his Spitzbergen material, including Rotylenchus, Pratylenchus and Paratylenchus. On the other hand, several microbe - feeding genera were much more dominant on Spitzbergen than in temperate regions, including Teratocephalus, Cervidellus and Plectus, as well as the primarily lower-plant feeding genus Tylenchus.

The relative roles of higher-plant parasites and lower-plant / microbe - feeders in the diverse temperate and tropical faunas are difficult to characterize. However, confirmed higher-plant parasites were dominant in some of these habitats. For example, the most common species found by Willard et al. (1973) in a natural grassland were Helicotylenchus leiocephalus, Xiphinema americanum, Tylenchorhynchus canalis, Paratylenchus tenuicaudatus and Pratylenchoides bacilisemenus. Yuen (1966) found that plant parasites accounted for 31 out of a total of 76 species, and contributed more than 50% of all individuals collected from another natural temperate grassland. Yuen noted that plant parasites were of similar importance in two cultivated areas studied by Winslow (In: Yuen, 1966).

Plant parasites were less important in the regenerated woodland Yuen studied, but still accounted for 19 out of 62 species, and contributed more than 30% of all individuals. Banage and Visser (1967) considered 7+ genera out of 31+ genera were plant feeders, which comprised 31% of all individuals in virgin bush in Uganda. Plant feeders were less important in other habitats, but still generally appeared more important than in high latitude environments (e.g. Wasilewska, 1971).

A feature of high arctic vegetation is the relative diversity of lower plants, including bryophytes, lichens and fungi. Bliss (1977c) lists only 96 species of vascular plants from Truelove Lowland, compared with 175 species of lichens (Richardson and Finegan, 1977), 132 species of mosses (Vitt and Pakarinen, 1977), and 92 species of fungi (Booth and Widden, 1977). Mackenzie Lamb (1970) noted a similar pattern in the flora of the Antarctic - "The terrestrial vegetation of Antarctica, in order of decreasing abundance of representation, consists of lichens, mosses, algae, hepatics, fungi and bacteria, and flowering plants".

Savile (1972) discussed the characteristics of lower plants that fit them for life in arctic environments. The apparent lack of competitiveness of bryophytes and lichens relative to higher plants appears unimportant in arctic environments, because higher plants are reduced in, or excluded from many habitats by physical conditions that the lower plants tolerate.

The arctic nematode fauna seems to reflect the primitive nature of the arctic flora. Evolutionarily advanced and specialized flowering plant parasites are absent (e.g. Meloidogyne, Heterodera). Plant parasites are present, but are represented primarily by the relatively primitive and unspecialized Tylenchoidea (e.g. Tylenchus) which, for the most part, are free-living in the soil and, in cases where they live in/on plants, generally attack lower plants. Relatively specialized insect and animal parasites also appear to be poorly represented in high latitude faunas (Mulvey, 1963, recorded one species of mermithid). Evidently the radiation of nematodes in response to the radiation of flowering plants, insects and vertebrates (Schafer, 1971) is poorly reflected in the arctic nematode fauna because, though these three groups now dominate most terrestrial environments, they do not dominate arctic habitats.

My review shows that microbe - feeding nematodes, as exemplified by the genus Plectus, dominate many high latitude faunas. There is little doubt that tundra sites support a diverse fauna of micro-organisms. For example, Truelove Lowland has a minimum of 108 species of bacteria (estimated from Widden, 1977). Dunican and Rosswall (1974) concluded that the range of heterotrophic bacteria in tundra soils parallels that in temperate mineral soils, and that no single group showed any preference for tundra environment. Similarly, Heal et al. (1967) found that in numbers of both species and individuals the testate amoebae fauna of Signy Island soils approximate to those of temperate woodland and moorland. Heal (In : Ryan, 1979) looked at soil protozoa from Truelove Lowland and concluded that "the ones here are common anywhere". Parinkina (1974) also stated that the total number of micro-organisms in tundra is not significantly different from the sizes of populations observed in temperate zones.

Microbe - feeding appears to be the primitive, generalized nematode feeding habit, and the microbial feeding groups likewise appear to best represent the morphologically primitive and unspecialized condition (i.e. the Torquentia - Andrāssy, 1976). While the Plectids may not be the most primitive of the Torquentia, they are close to the stock from which the other two nematode lines developed (i.e. the Secernentia and Penetrantia), with their development of parasitism and massive radiation of both parasitic and non-parasitic species (Andrāssy, op. cit.).

The dorylaimids which, like the plectids, make an important contribution to arctic faunas, are considered by Andrāssy (1976) to be among the most recent nematode groups phylogenetically (i.e. the Penetrantia). The dorylaimids include both parasites and non-parasites, but the genera best represented in the arctic (e.g. Dorylaimus, Eudorylaimus) seem to represent a new radiation of non-parasitic generalists, which individually are able to feed on a very wide range of organisms, including other nematodes. The occurrence of dorylaimids in relative abundance, and in a greater variety of lower latitude habitats than plectids (e.g. Tables 2 and 3), may reflect their presumed higher level of effectiveness as generalists.

Other major invertebrate groups in high latitudes may show similar emphasis on primitive and/or relatively generalized component taxa. Janetschek (1970) believes there is a sequence and prevalence of mite and collembola taxa within the high Antarctic itself. Mites especially show a latitudinal sequence corresponding to habitat development. The pioneering Trombidiformes (Prostigmata), represented by the families Pachygnathidae, Tydeidae and Eupodidae, are most southerly in occurrence. The predatory Rhadididae first appear relatively far north, in South Victoria Land. Oribatid mites (Cryptostigmata) only appear in North Victoria Land, despite being quite common in the outer Maritime Antarctic. The Collembola also belong to a few families which are also pioneers elsewhere (Onychiuridae, Hypogastruridae, Isotomidae).

To conclude : high latitude and low latitude nematode faunas differ primarily in relative dominance of different components of the faunas. In high latitudes relatively primitive nematodes appear to dominate. In this regard there appears to be a correlation between the nematode fauna (and invertebrate fauna as a whole) and high latitude floras, which also have a large primitive component. High latitude communities, in addition to being relatively simple, appear primitive in an evolutionary sense, since they are dominated by floral/faunal elements that presumably dominated communities preceeding those which developed from the evolution and radiation of higher plants, insects and terrestrial vertebrates.

2.3.2 Hypothetical Mechanisms Governing Species Diversity

Having gained an idea of the composition of high latitude nematode faunas, it is time to address the three questions posed in the introduction to this chapter. Pianka (1978) lists ten hypothetical mechanisms for determining species diversity : (1) evolutionary time; (2) ecological time; (3) climatic stability; (4) climatic predictability; (5) spatial heterogenity; (6) productivity; (7) stability of primary production; (8) competition; (9) rarefaction; and (10) predation.

2.3.2.1 Evolutionary Time

The evolutionary time theory assumes that community diversity increases with age. For example, temperate regions are considered impoverished due to recent glaciations (Fischer, 1960). Given sufficient time for speciation and evolution, appropriate organisms will occupy these newly opened habitats.

Northern Hemisphere tundras developed in the pleistocene (Dorf, 1960) and the first definitely determined tundra appeared 1 million years ago (Hopkins, 1974). Consequently, tundra floras and faunas have had little time to evolve. Tundra floras (Yurtsev, 1972) and faunas (Hoffman and Taber, 1967) probably evolved first in the Holarctic highlands of Central Asia and the Rocky Mountains. Hoffman and Taber (op. cit.) believe that arctic lowland faunas probably originated in Central Eurasia when tundra replaced cold-temperate steppe and taiga during the Pleistocene. These animals, preadapted to cold winter environments, were able to evolve populations capable of surviving in the new lowland tundra environments.

Downes (1964, 1965) and Ryan (1979) discussed the origins of tundra invertebrate faunas in general and concluded that they have been derived by reduction from southern faunas. There are few endemic arctic invertebrate species. The arctic soil nematode fauna shares many species with lower latitude faunas. Cobb (1921) noted that about 50 per cent of the species from the Canadian Arctic and Alaska are common much further south, many occurring in the vicinity of Washington, D.C., and in the Tropics.

Simpson (1964) believes that temperate zones have probably existed for as long as tropical ones, having simply shifted with their floras and faunas in response to glacial advance and retreat. If this is true, organisms adapted to cold winter environments have existed for a very long time. Simpson feels that if the time theory were correct, the steepest gradient in species diversities should occur in the recently deglaciated temperate zones. Since, for North American mammals at least, this zone shows a fairly flat diversity profile, there is some evidence against the evolutionary time theory. Because very recent arctic and temperate habitats have high nematode species diversities, and many cosmopolitan species, Simpson's arguments against the evolutionary time theory gain additional support.

2.3.2.2 Ecological Time

This theory resembles the evolutionary time theory, but is concerned with the shorter time available for dispersal. The large cosmopolitan element of recent arctic nematode faunas (Cobb, 1921), and of geographically isolated non-arctic faunas (e.g. Yeates, 1973), indicate that the dispersal powers of nematodes are sufficient to make ecological time an unimportant barrier to high nematode diversity in most communities.

Although soil living nematodes have limited powers of dispersal through active migration - in the order of metres per year (Wallace, 1963) - they have considerable potential for long distance passive dispersal, partly because of their small size, but primarily because of their widely shared cryptobiotic capabilities in response to adverse physical and chemical conditions, including desiccation (cf. Evans and Perry, 1976). These characteristics allow them to be dispersed by diverse agents, including wind (White, 1953; Orr and Newton, 1971), water (Thompson et al., 1949; Meagher, 1967), insects (Poinar, 1975) and birds (Epps, 1971; Spaull, 1973b). Wallace (1963) cites examples of dispersal of plant parasitic nematodes in association with plants. Several soil living nematode groups have established phoretic relationships with insects, where the insect serves only as a means of transport for the nematode. Poinar (1975) notes that members of the Cephalobidae, Aphelenchidae, Aphelenchoididae, Dorylaimidae, Neotylenchidae, Monochidae, Tylenchidae, and others, have phoretic associations with insects. The role of other organisms in spreading nematodes is less clear, but migratory mammals (e.g. caribou) and birds (e.g. geese, terns) are probably important long distance dispersal agents, particularly in the arctic. Spaull (1973b) notes that the sheathbill, the only land bird in the maritime Antarctic, has been observed to carry live soil nematodes in dried mud on its feet.

Arctic regions appear to offer unique dispersal opportunities for organisms with limited active dispersal capabilities, which may help account for the wide distributions of many arctic plants and animals. Savile (1972) believes that winter wind dispersal over ice (and across plains) is the most important long distance dispersal mechanism of arctic plants. Unbroken ice in conjunction with frequent high winds offers potential for rapid long-distance dispersal between arctic land areas that is unlikely to be matched for land surrounded by ice-free seas. Savile (op. cit.) notes that this is not a completely haphazard means of dispersal, because all material carried across sea ice (or frozen lake or plain) tends to accumulate below cliffs or similar obstructions. Viable plant material deposited by eddies near the base of such obstructions is accompanied by snow, mineral soil and plant fragments. These sites are accordingly wellwatered, both by melting snow and by seepage; they accumulate soil and humus, and they are among the most favourable sites for plant growth. Savile's conclusions appear equally applicable to nematodes and particularly to those that often live closely associated with lower plants, such as Plectus.

Water dispersal may also be important in the Arctic, particularly for aquatic organisms which are relatively inaccessible for wind dispersal. The Arctic Ocean is small in area relative to the volume of freshwater discharged into it each summer. Presumably large amounts of organic and inorganic material, together with living organisms, will be carried by currents from one arctic land mass to most others within several years (cf. H.O. Pub. No. 705, 1958).

I earlier pointed out that nematode diversity is lower in the Antarctic than in the Arctic (Antarctic invertebrate diversity, excluding nematodes, is proportionately even more reduced). Although historical geological occurrences, or the relative harshness of the environment, may better account for the lower diversity of antarctic communities, arctic dispersal methods will be either less effective, or inoperable in antarctic regions. Large areas of ice-free ocean separate the Antarctic from most possible floral and faunal sources. The great circumpolar winds, with little land beneath them, may also be a barrier to most aerial organisms that might disperse or migrate south (Spaull, 1973b). The high proportion of marine vertebrates in the Antarctic vertebrate fauna indicates the ineffectiveness of arctic dispersal methods for terrestrial vertebrates. The presence of endemic Antarctic genera in most of the lower plant groups (Llano, 1965), and high endemism in oribatid mites on the Antarctic continent but not in the Maritime zone (Wallwork, 1967), also suggests relative inaccessibility to terrestrial organisms.

It is not yet clear whether the Antarctic continent has a highly endemic nematode fauna (cf. Timm, 1971; Spaull, 1973b), but the dispersal capabilities of nematodes, in which they appear more akin to micro-organisms than to most invertebrates, may make the continent more accessible to them than to most invertebrates.

2.3.2.3 Climatic Stability and Climatic Predictability

Proponents of climate as a determinant of community diversity include Klopfer (1959), and Fischer (1960). Exploitation of environments with unstable/unpredictable climates requires that the organisms have broad tolerance limits to cope with the wide range of environmental conditions they encounter. By requiring generalization, variable environments favour organisms with broad niches, which reduces species diversity. Conversely, environments with stable/predictable climates permit finer specialization and narrow niches, and thereby allow greater species diversity.

It is evident that high latitude climates are particularly restrictive for terrestrial vertebrates that remain throughout the year, but these conditions are not as limiting for soil living invertebrates that are active only in the summer. Furthermore, invertebrates in high latitudes do not have to adapt to large diurnal temperature variation, often accompanied by freezing, as they do in temperate and alpine environments. Consequently, the arctic summer, though cool, offers a relatively benign climate. A more important limitation of high latitude summers is their shortness, which probably excludes many invertebrates committed to annual life cycles (Downes,1964).

The ability of many nematodes to tolerate unfavourable environmental conditions, including freezing and desiccation, has been well documented (e.g. Cooper and

Van Gundy, 1971; Wallace, 1976), although the mechanisms by which these abilities are achieved are poorly understood. Because the tolerant dormant condition is readily reversed by the return of favourable conditions, nematodes are equipped to utilize intermittently favourable environments, including those in which the growing season is shorter than the nematodes' generation times. In this regard nematodes may be considered an invertebrate analogue of lichens, which can resume full activity from a desiccated condition within approximately a minute (nematodes require more time). Thus lichens withstand the arctic winter with impunity, and can make the most of brief opportunities for growth in the bleakest arctic summers (Savile, 1972).

The above discussion shows that nematodes have the broad adaptive capabilities to function effectively in high latitude climates, but does not explain their high diversity despite their presumed broad niche requirements. I consider this problem in later sections of this chapter.

2.3.2.4 Spatial Heterogeneity

Proponents of the theory of spatial heterogeneity believe there is a general increase in environmental complexity towards the tropics (Pianka, 1978). Because spatially heterogeneous environments have more resources, they usually support more species than do homogeneous environments; hence tropical habitats generally support more species than do temperate and high latitude habitats.

This theory has two subcategories, one on a macro-scale, the other on a micro-scale. Simpson (1964) calls the first topographical relief, and shows that greater relief increases the variety of ecological conditions, and hence ecological niches in a region. The component of total diversity due to topographical relief and number of habitats does increase towards the tropics, particularly for birds and mammals (i.e. mountains in the tropics have temperate and alpine environments). However, this subtheory is of limited value in explaining soil nematode global diversity patterns because being very small, nematodes encounter the world in a much more 'coarse grained' way than do larger organisms (Pianka, 1978).

Micro-spatial heterogeneity is local in scale, with the size of the environmental elements corresponding roughly to the size of the organisms populating the region. Elements of the environmental complex in this class might be soil particle size, rocks and boulders, karst topography or the pattern and complexity of vegetation. One of the few studies which relates species diversity to micro-spatial heterogeneity is that of MacArthur and MacArthur (1961), who showed that foliage height diversity is a good predictor of bird species diversity.

In contrast to macro-spatial heterogeneity, there is little reason to suppose that micro-spatial heterogeneity of the soil environment declines with increasing latitude. Consideration of the Truelove Lowland soil environment emphasizes this point. An outstanding feature of the lowland is its microtopographic, microclimatic, vegetative and temporal heterogeneity, despite its small area and low relief. Because of recent postglacial uplift, the lowland consists of a succession of progressively older raised beach ridges, ranging from the presently active beach, to the oldest fossil beach dated ca. 9,450 years B.P. (Barr, 1971). Accompanying the succession of beaches is change in the chemical environment (e.g. salinity), progressive development of soil, and change in, and development of the vegetation (Wasilewska, 1971, found differences in nematode species composition in early and late stages of succession in a sand dune forest, which increased overall diversity in the forest). Interspersed with the raised beaches are lakes, low-lying sedge meadows and rock outcrops which, combined with the raised beaches, provide a continuous range of environments from permanent lakes to desert.

Superimposed upon this mosaic of environments is additional topographical diversity associated with patterned ground caused by frost action (e.g. hummocky meadows, frost-boil meadows, ice-wedge polygons - Muc and Bliss, 1977). Patterned ground which occurs chiefly in cold climates, makes an important contribution to micro-spatial heterogeneity in tundra regions (e.g. Chernov *et al.*, 1975a; Bunnell *et al.*, 1975), and clearly affects the distribution and abundance of plants (Tikhomirov, 1974), micro-organisms (Parinkina, 1974) and soil invertebrates (Chernov *et al.*, 1975b).

From the perspective of small soil inhabiting organisms, the Truelove Lowland in particular, and tundra environments in general, offer a level of micro-spatial heterogeneity that is probably rarely exceeded, or even matched, by similar-sized areas of temperate grassland, tropical savanna, or even tropical rainforest. I consider that the micro-spatial heterogeneity of high latitude soil environments is a major factor in explaining the high diversity of soil living nematodes in these environments, and the preponderance of soil invertebrates in general (*cf*. Ryan, 1977c).

While high latitude soil environments show high micro-spatial diversity, vegetation height diversity is very reduced compared with low latitude environments. Consequently, for invertebrates which live on or above the soil surface, the number of niches is small. The situation is analogous to that facing birds in grassland compared with tropical rain forest, in terms of the number of available niches. I believe that lack of vertical diversity in the vegetation is one cause of the reduced invertebrate fauna in the arctic (cf. Ryan, 1977c).

2.3.2.5 Productivity and Stability of Production

Connell and Orias (1964) have made the most complete statement of the productivity hypotheses. In unproductive habitats, animals may have to take all the food they encounter, but in productive habitats they can be more selective. Consequently, more productive environments allow greater specialization, and the same spectrum of food types can support more species. In stable environments animals require less energy for maintenance, and have more energy available for production. This results in larger populations, which have greater genetic diversity. Greater genetic diversity increases the range of habitats occupied, which increases the chance for genetic isolation between populations, and therefore increases the likelihood of speciation. More species increase community complexity and, through positive feedback, make the environment more stable.

I have shown that microbial-feeding nematodes dominate high latitude terrestrial nematode faunas. I have also cited evidence that the species diversity and numbers of individuals of micro-organisms is high, and probably comparable with those of lower latitudes. Furthermore, production of micro-organisms in high latitudes may be comparable with that of other biomes during the biologically active period, though not on an annual basis. Parinkina (1974) reviewed tundra microbial production information, and concluded that "microbial productivity in biologically active tundra soils is commensurable with that in the soils of more southern biomes". Booth (1977) estimated the percent primary production utilized by heterotrophic organisms in different biomes, and obtained a value of 62% for xeric forests, 65% for prairies, 76% for mesic forests, and 90% for tundra sites. Since herbivory probably accounts for a relatively small proportion of heterotrophic activity in tundra environments (Bliss, 1977b), microorganisms appear responsible for a relatively high proportion of tundra heterotrophic activity. Booth concluded that decomposable substrates are colonized more rapidly in tundra environments than in any of the other biomes, which points to a rapid tie-up of nutrients over short physical distances by tundra decomposing populations.

It is clear that microbial production can be both diverse and high in some high latitude environments, which the nematode fauna presumably reflects. Having made this point, it is important tc establish that nematodes are better equipped than most invertebrates to utilize habitats with diverse but low productivity, and habitats with unpredictable productivity, because some high latitude environments undoubtedly can be characterized in these terms (e.g. polar desert - which is represented by the crest habitat in my study).

Polyphagy is clearly one attribute which fits animals for habitats with low/uncertain productivity. Most nematodes are highly polyphagous (Dao, 1970). For example, the plant parasite *Pratylenchus penetrans* reproduced on each of 182 plants tested (Oostenbrink, 1957). Furthermore, nematodes endemic in one climate zone are not restricted to plants of that zone. Sharma (1968) showed that many tropical plants are excellent hosts for *Tylenchorhynchus dubius*, which is widespread in the Netherlands and is evidently limited to temperate zones. Primarily free-living fungal-feeding nematodes of the genera *Aphelenchoides*, *Aphelenchus* and *Ditylenchus* also have unspecialized feeding habits. *Aphelenchus avenae* has been cultured on 54 different fungi, as well as plant callus (Dropkin, 1966). Microbial-feeding nematodes show similar diversity. *Dorylaimus etterbergensis* feeds on fungal spores, algae, ciliate cysts, and other nematodes, in addition to bacteria (Hollis, 1957). Likewise, *Mononchus potohikus* can be reared on bacteria, or on other nematodes (Yeates, 1969).

Another important adaptive characteristic of nematodes is their ability to persist at very low population densities. In many species (e.g. plectids) males are either rare or unknown, and reproduction is by parthenogenesis (cf. Goodey and Goodey, 1963; Triantaphyllou, 1971). These species are therefore not obliged, unlike self-perpetuating sexually reproducing populations, to maintain a minimum population density determined by the maximum distance reproductive individuals must travel to contact each other. Consequently, the mimimum density of resources able to support asexually reproducing individuals can be lower than the density of resources required by sexually reproducing populations. In this context, Spaull (1973b) noted that at Alamode Island, the most southerly maritime antarctic island he investigated, males were rare or absent in approximately 75 per cent of the nematode genera, while the corresponding figure for Signy Island, the most northerly island he studied, was less than 50 per cent. However, there were no production data associated with this information.

To summarize : the capacity of many soil living nematodes for polyphagy, their ability to maintain low population densities, and their flexible responses to variable environmental conditions, give them the potential to maintain high diversity in environments whose resources seem, at first sight, severly limiting in terms of modern theories of species diversity in relation to resource availability.

Current theories of diversity in relation to resources probably explain the absence of some invertebrates from high latitudes. For example, hymenoptera with higly developed social systems (i.e. Aprocrita) are represented at Truelove Lowland by one species of *Bombus* (Ryan, 1977b). Evidently the few flowering plants present are insufficient to support what is a very efficient resource gathering system in more productive environments.

2.3.2.6 Competition

Proponents of the competition theory of diversity include Dobzhansky (1950) and Williams (1964). In diverse and stable communities, such as tropical rain forest populations are thought to be often near their maximum sizes (equilibrium populations), with the result that competition is strong. In these communities selection is for competitive ability ('K selection'), and successful organisms have narrow, well-defined zones of competitive superiority. The resulting small niches make high diversity possible. In contrast, populations in temperate and polar communities are considered less stable and often below maximum size. In such communities it is the phsyical world to which organisms must adapt, so that successful organisms have broad niches, which reduces diversity. Because these communities are unsaturated with individuals, competition is weak or absent, and selection is for rapid reproduction ('r selection').

May and MacArthur (1972), and May (1974), showed that there is an effective limit to niche overlap in the real world, and that this minimum niche separation distance, measured by the ratio between interspecific niche separation and intraspecific niche breadth, d/w, is around 1-2. While intraspecific niche width is presumably a function of environmental fluctuation (but see below), this limit to niche overlap is insensitive to the degree of environmental fluctuation, unless it is very severe (e.g. as in polar environments), when species packing becomes roughly inversely proportional to the environmental variance. Another pertinent discovery was made by MacArthur and Levine (1967) who showed that when the distance between the resource optima of the resident species is smaller than a certain value, a community is closed to invasion. They called this value a 'limiting similarity' in the sense that there is a limit to the similarity of the residents consistent with the community still being invasible.

Nematodes evidently are 'r strategists', with their very broad food and habitat niches, small body size, short life span, and high intrinsic rate of increase (see Chapter 5). However, despite being 'r strategists', nematodes maintain high diversity and densities in high latitudes, and thereby constitute an anomaly in regard to the above theoretical treatments.

Roughgarden (1974) pointed out that the analyses of May and MacArthur (1972), and MacArthur and Levins (1967) considered only utilization curves with thin tails (i.e. platykurtic curves). The platykurtic curve represents the utilization curve of a specialist species which is finely tuned to exploit a specific and narrow set of resources. Roughgarden (op. cit.) extended the above analyses to thick-tailed (i.e. leptokurtic) curves, which is the form of utilization curve shown by generalist species.

He concluded that much closer species packing is possible (i.e. $d/w \ll 1\text{-}2$) when the utilization curves are leptokurtic. Furthermore, the phenomenon of limiting similarity is conspicuous only when the utilization curves are platykurtic. The community remains open to invasion even though the resident species are very similar, providing that the utilization curves are leptokurtic. Roughgarden related his mathematical analysis to assemblages of coral reef fishes, and tropical fruit- and flower-eating birds, and found that closely related generalist species may show very close packing. Yoshiyama and Roughgarden (1977) extended Roughgarden's analysis to show that increasing niche dimensionality allows even closer species packing.

While Roughgarden (1974) and Yoshiyama and Roughgarden (1977), offered a possible explanation for the diversity of nematodes in high latitudes in terms of theories of niche overlap (the high diversity of marine nematode guilds is well established, e.g. De Bovée, 1975; Heip and Decraemer, 1974), their ideas have wider implications. Evidently, groups of closely related generalists occur in stable tropical environments, and may establish closer species packing than do specialists in the same environments. This possibility poses an important contradiction to the general theory outlined in the first paragraph of this section, which supposes that close packing in the tropics is a result of narrow niches. Roughgarden (op. cit.) speculated that groups of closely related generalist species may be formed when taxa are rapidly evolving. Assuming that tropical organisms are not static in an evolutionary sense, despite their diversity and density, and accepting that evolving guilds of generalists can attain closer species packing than do specialists, tropical communities need not have attained maximum species diversity.

The relative diversity of nematodes compared with other invertebrates in temperate and polar environments may be explained in terms of competition with other invertebrates. As 'r selected' generalists, nematodes may be at a competitive disadvantage in tropical invertebrate faunas that are presumably dominated by 'K selected' specialists. As one proceeds from tropical to temperate environments, the proportion of 'K selected' invertebrates will decline, thereby reducing competitive pressure on nematodes, (i.e. 'ecological release' - Pianka, 1978). This argument may be particularly pertinent in explaining the high diversity and densities of plant parasitic nematodes in temperate habitats. 'K selected' invertebrates are largely absent in high latitudes, and 'r selected' invertebrates are much reduced. Consequently, nematodes probably experience little competition from other invertebrates in high latitudes.

2.3.2.7 Rarefaction and Predation

Rarefaction refers to the density-independent removal of organisms from a community. In communities that are not fully saturated with individuals, competition is reduced and co-existence is possible without competitive exclusion. Consequently, communities can be oversaturated with species, in the sense that more species can co-exist than would be possible if the community were fully saturated with individuals (Pianka, 1978). Predators can act as rarefying agents, either by random or selective removal of competing prey species, thereby allowing co-existence of species that might be eliminated by competitive exclusion in the absence of the predator (Abrams, 1977; Paine, 1966; Harper, 1969). Both rarefaction and predation effectively increase allowable niche overlap, and thereby allow closer species packing.

Because nematodes can survive a very wide range of physical environmental factors, common rarefaction phenomena, such as prolonged winter, or unseasonal cold during the summer, are unlikely to seriously affect them. While I have little information with direct bearing on this matter, data I obtained on nematode densities during my study indicate that there is little winter mortality; as densities were high at spring thaw as they were in the preceeding fall (Chapter 3). The small difference in densities between seasons appeared to be correlated with seasonal difference in primary production.

The role of predation in governing the diversity of high latitude nematode faunas is also difficult to assess. Small soil arthropods that feed on nematodes include collembola (Brown, 1954; Murphy and Doncaster, 1957), tardigrades (Doncaster and Hooper, 1961; Sayre, 1969), and mites (Rodriguez, Wade and Wells, 1962), each of which is important in high latitude environments (*cf*. Ryan, 1977a). Ciliates (Doncaster and Hooper, *op*. *cit*.), sporozoa (Williams, 1967), and fungi (Duddington, 1955) also attack nematodes. However, the effects of these organisms on the numbers of nematodes in the soil is unknown. Possibly the most important predators of nematodes in high latitudes are other nematodes. The numerical importance of dorylaimids in high latitude faunas may be important in this respect, because many dorylaimids feed on other nematodes. Whether predatory nematodes increase diversity by acting as rarefying agents is unclear, but they have undoubtedly increased diversity by expanding into another trophic level. Since microbial-feeding nematodes contribute a large proportion of invertebrate standing crop and production in high latitude environments, it seems sound evolutionary strategy for predatory nematodes to exploit other nematodes in this manner.

2.3.3 Nematode Global Distribution Patterns - An Overview

As one proceeds from the equator to the poles, soil living nematodes show three major trends in species diversity and densities. Firstly, higher plant parasitic nematodes increase in diversity and density from tropical to temperate regions, and then decreases sharply from temperate to polar regions. Secondly, lower plant feeding and microbial feeding nematodes also show some increase from the tropics to temperate regions but, unlike the higher plant parasites, maintain high diversity and densities far into polar regions. Thirdly, Arctic regions have higher nematode diversity than do Antarctic regions.

A review of various theories purporting to explain species diversity patterns suggested several causes for these nematode distribution patterns. Higher plant parasitic nematode diversity in tropical environments may be kept relatively low by competition with a diverse fauna of other, more specialized, herbivores. The loss of specialized tropical competitors from temperate faunas may help account for the increased diversity of higher plant feeding nematodes in temperate biomes. Another important influence on nematode diversity and densities in temperate regions may be man's agricultural activities, including the breeding of many new varieties of plants, monocultures, and transport of agricultural materials. The relative unimportance of higher plant parasitic nematodes in polar regions simply reflects the unimportance of higher plants in these regions.

The relative diversity and abundance of lower plant feeding and microbial feeding nematodes in tropical and temperate regions is probably governed by the same factors, apart from man's agricultural activities, that affect higher plant parasites. However, different factors become important in polar regions. Soil micro-habitat diversity is an important determinant of nematode diversity, and high latitude environments may match or exceed lower latitude environments in this regard. Also, lower plants and micro-organisms, unlike higher plants, maintain high diversity and densities in high latitudes. These factors, in combination with the broad adaptive abilities shared by many nematodes, and relative lack of competitors, account for the high diversity and densities of these nematodes in high latitudes.

Lack of nearby faunal sources, and very restricted opportunities for dispersal in the Antarctic compared with the Arctic, probably account in part for the relatively small nematode fauna in the Antarctic. Harsher climatic conditions, with consequent reduction in the general flora and fauna, doubtlessly also contribute to the reduced nematode fauna in this region.

The general trends in nematode diversity and abundance from the equator to the poles are probably paralleled by similar trends in the nematode fauna as one procedes from low to high altitudes in the tropics.

Chapter 3

NEMATODE DENSITIES

3.1 Introduction

In this Chapter I present estimates of nematode densities in the four study sites for July and August, 1972, and for June to September, 1973. I correlated densities with biotic and abiotic environmental factors characterizing each study site, drawing on pertinent research presented in Bliss (1977). I also interpreted the four study sites as representative of different widely occurring arctic environments (after Bliss, 1977a; Muc, 1977; Svoboda, 1977), and I used the density/study site associations to predict nematode densities in some major arctic environments. Finally, I compared nematode densities in arctic environments with densities in habitats in other biomes.

3.2 Methods

I established five 5 x 5 m quadrats in the Intensive Meadow site (Hummocky Sedge-moss Meadow - Muc, 1977), and 15 in the Intensive Raised Beach site (I.R.B.). The I.R.B. quadrats were evenly distributed between the Crest, Slope and Transition zones (Svoboda, 1977). The same quadrats were used both years.

I began sampling both years when the active layer was approximately 5 cm deep. Initially in 1972 the samples were collected on every third day. I took twenty samples on each sampling date, one from each quadrat. I used a 6 cm diameter bulb planter to obtain the samples, which I randomly selected from a grid of 6 x 6 cm squares in each quadrat. The samples were 5 cm deep, giving a soil volume of approximately 140 cc.

I took an additional 32 samples to a depth of 10 cm from beneath the 5 cm deep samples, four on each sampling date from 24 July to 14 August, 1973. These 5-10 cm deep samples, which were randomly selected from the locations of the 5 cm deep samples, were also evenly distributed between the four study areas.

I extracted the samples using the 'tray method' of Whitehead and Hemming (1965). In this method the material is spread over double layers of tissue paper supported on insect screening in 28 x 22 cm plastic-coated wire baskets standing in 30 x 27 x 5 cm plastic dishes. Water is then added to the dishes until the soil becomes wet, and the baskets are left in place for 24 hours. I extracted thirty two of these samples for a second 24 hours.

The nematode suspensions (ca. 1 L) I obtained from the collecting dishes I concentrated into 3 dram vials using 40 cm high x 5 cm diameter glass cylinders. The vials were attached to the tapered bottoms of the cylinders with rubber tubing and screw clamps. A tight fitting rubber plunger run through the cylinders every 2 to 3 hours prevented nematodes settling on the cylinder sides.

I allowed the suspension to settle for approximately 12 h. The concentrated nematodes were heat-killed and stored in a formalin-glycerol fixative (Southey, 1970).

The extraction efficiency of the 'tray method' was determined by returning counted live nematodes to autoclaved soil (20 min at 15 psi and 245°C). I re-extracted these nematodes for two successive 24 h periods.

Counting was done at 25x under a stereo microscope in 120 mm diameter x 20 mm high glass dishes. The dishes were marked into eighths, and I counted a single eighth from each sample. When a subsample contained less than 50 nematodes, I counted an additional subsample, and used the mean of the two subsamples.

3.3 Results

3.3.1 Efficiency and Rate of Extraction

Extraction efficiency was 34.4% after 24 hr, and 42.3% after 48 hr (Table 4). Numbers extracted during the second 24 hr averaged 27.7% of the numbers collected during the first 24 hr. The soils of the four study sites had similar extraction rates, and standard deviations were uniformly high (Table 5).

3.3.2 Densities at 0-5 cm Soil Depth

In 1972 the transition had the largest seasonal mean density and the meadow had the smallest (Table 6). Furthermore, densities increased progressively from the crest, through the slope, to the transition zone. All four study sites had relatively low densities at the start of the season, which increased quickly as the season progressed (Fig. 3).

The four sites showed the same relative densities in 1973 that were observed in 1972, except for the fact that the slope mean was slightly larger than that of the transition (Table 6). The 1973 densities were larger than the equivalent 1972 values, except for the transition, which was a little larger in 1972. In contrast to 1972, the 1973 densities were high when sampling began, and either remained high or declined as the season progressed (Fig. 3).

I compared densities within years using the t-test (Li, 1964). Except when the slope and transition are

Table 4. Results of extraction efficiency studies. Given are nematode numbers returned to autoclaved soil, numbers recovered during first and second 24 h, and total recovery. (n = 8 for means and percentages).

	Numbers recovered		
	mean	± SD	%
Initial	10040	8539	-
0-24 h	3917	4394	34.4
24-48 h	830	779	8.0
0-48 h	4747	5155	42.4
24-48 h X 100/0-24 h			27.7

Table 5. Numbers of nematode extracted from autoclaved soil during two 24 h extraction periods (N = 8 for numbers extracted and for percentages).

Habitat	Crest		Slope		Transition		Meadow	
	Number extracted							
	Mean	± SD	Mean	± SD	Mean	± SD	Mean	± SD
0-24 h	2570	1533	2700	939	2840	927	798	312
24-48 h	604	401	717	552	904	698	246	280
$\frac{\text{0-24h} \times 100}{\text{24-48h}}$	29.4		28.5		31.6		28.5	

Table 6. The 1972 and 1973 seasonal maximum, minimum and mean numbers of nematodes m^{-2} at 0 - 5 cm soil depth for the four habitats. n is given in parentheses.

	Number m^{-2} $(x10^6)$			
Range	Crest	Slope	Transition	Meadow
1972				
Max	5.520	8.492	9.303	2.868
Min	0.055	0.120	1.151	0.008
Mean	1.983(64)	3.009(64)	3.770(59)	1.008(59)
± SD	1.357	1.814	1.857	0.761
1973				
Max	10.992	10.734	9.658	3.557
Min	0.077	0.206	0.947	0.177
Mean	2.736(145)	3.621(145)	3.573(145)	1.168(142)
± SD	1.717	1.835	1.586	0.817

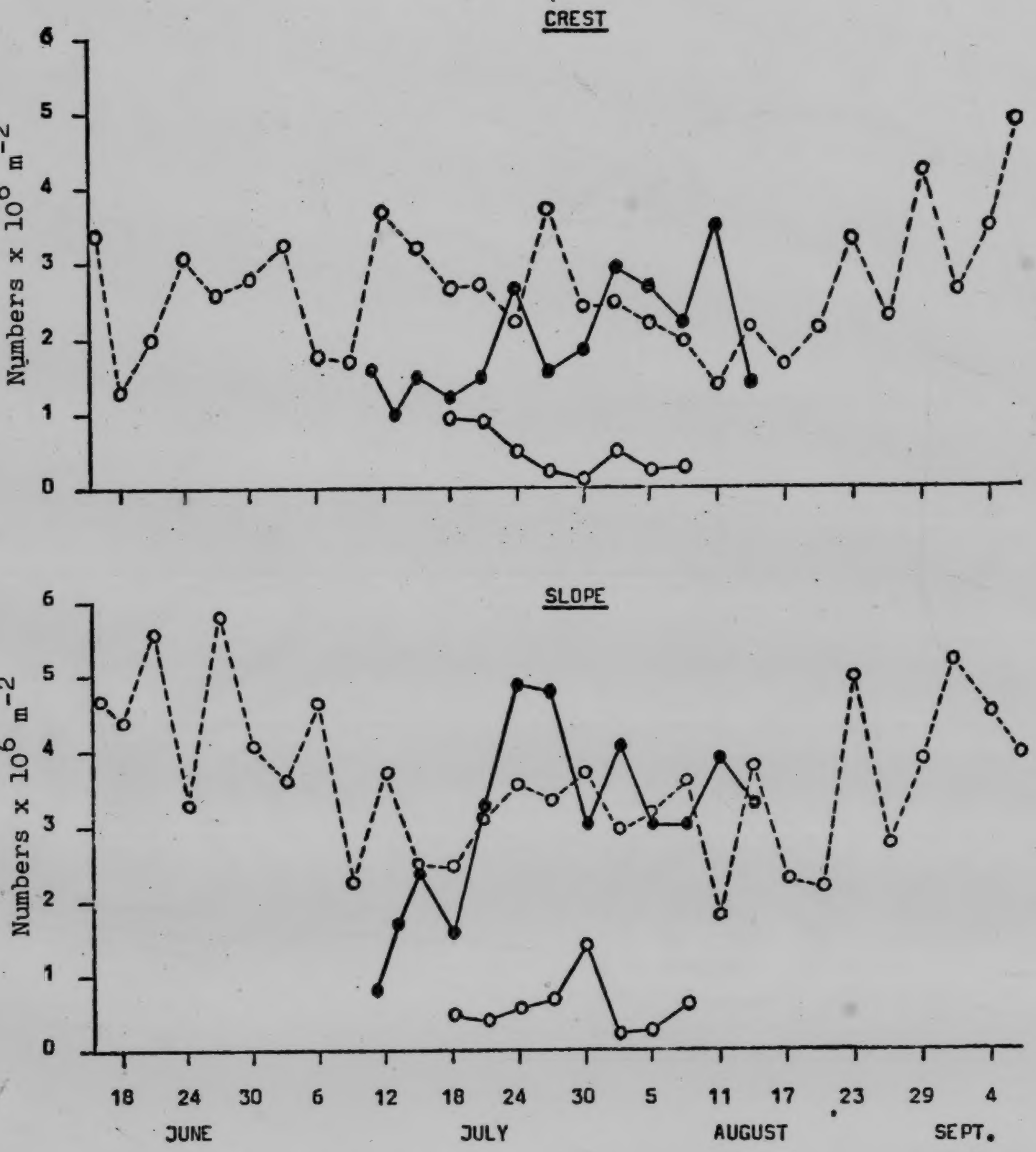


Fig. 3. The 1972 and 1973 seasonal numbers of nematodes m^{-2} at 0-5 cm soil depth, and 5-10 cm depth, for Crest, Slope, Transition and Meadow. Each point is the mean of 5 samples. (1972, 0-5 cm = ●—●; 1973, 0-5 cm = O---O; 1973, 5-10 cm = O—O.).

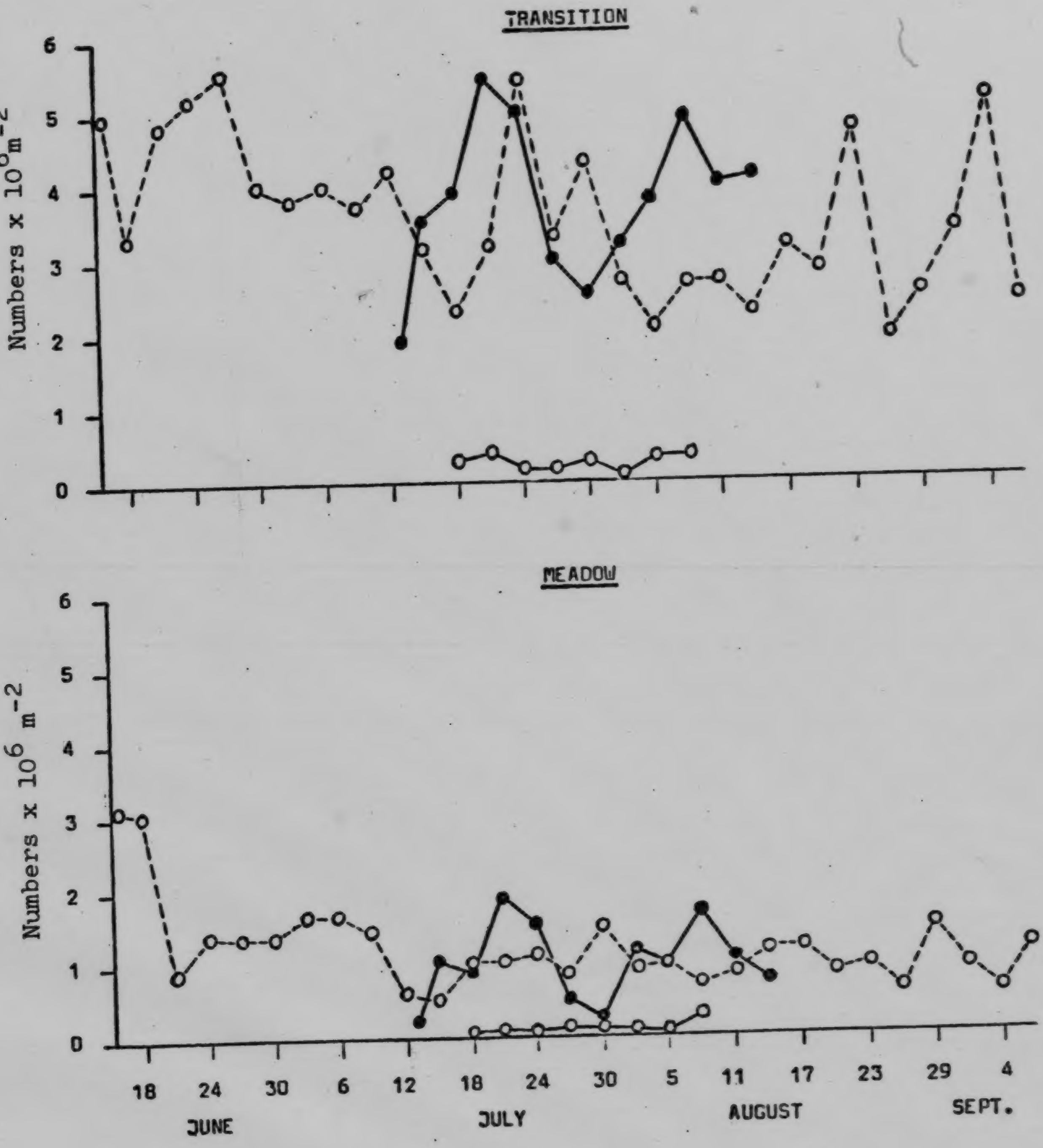


Fig. 3. Continued.

compared, all densities were different (p = 0.01) for both years. The transition density was larger than that of the slope at p = 0.05 in 1972, while these densities showed no difference at this confidence level in 1973.

3.3.3 Densities at 5 - 10 cm Soil Depth

At 5 - 10 cm soil depth the slope had the largest seasonal mean, followed by progressively smaller values in the crest, transition and meadow (Table 7). The crest had the largest proportion of total nematode population in the vertical profile at 5 - 10 cm depth (29.5%), followed by slope (15.7%), meadow (13.5%) and transition (9.1%). The crest and slope proportions were larger than that of the transition at p = 0.05.

3.3.4 Densities in the Top 10 cm of Soil

The 1972 seasonal mean numbers of nematodes in the top 10 cm of soil ranged from a high of 4,706,000 (slope) to 1,564,000 (meadow) (Table 8). The combined seasonal mean was substantially larger in 1973.

Table 7. The 1973 seasonal maximum, minimum and mean numbers of nematodes m^{-2} at 5 - 10 cm depth for the four habitats (n = 8 for means).

		Number m^{-2}	(x10^6)	
Range	Crest	Slope	Transition	Meadow
Max	0.963	0.947	0.391	0.309
Min	0.124	0.239	0.082	0.012
Mean	0.479	0.533	0.276	0.105
± SD	0.313	0.227	0.107	0.093

Table 8. The 1972 and 1973 seasonal mean numbers of nematodes m^{-2} in the top 10 cm of soil in the four habitats.

	1972	1973
	Number $m^{-2} \times 10^6$	
Crest	2.557	3.533
Slope	3.902	4.658
Trans.	4.706	4.631
Meadow	1.301	1.564
Mean	3.117	3.597

3.4 Discussion

3.4.1 Efficiency and Rate of Extraction

In their study of extraction Whitehead and Hemming (1965) collected 'few' additional nematodes when they continued extraction beyond 24 hr. Using the same method, I increased initial recovery by 29.5% when I extracted for an additional 24 hr (Table 5). When the maximum number of nematodes is wanted, the extraction period should be extended.

More important is the efficiency of extraction. I obtained a 34.4% recovery after 24 hr (Table 4). Using a centrifugal-flotation method, Willard (1972) obtained an efficiency of 36.5% for heavy clay soils.

These studies show that if extraction efficiency is not determined, estimates of nematode numbers may be very conservative (*cf*. Lagerlof *et al*., 1975). Estimates presented in this thesis are corrected for extraction efficiency.

3.4.2 Densities at 0 - 5 cm Soil Depth

The increase in nematode numbers from crest, through slope, to transition (Table 6) is correlated with the progressive increase in the amount of vegetation in these sites (Table 9), although most of the nematodes probably feed on the associated micro-organisms . The meadow did not fit this pattern, and had the largest plant biomass and smallest number of nematodes of the four sites.

Table 9. Average annual percentage plant cover, standing crop, net production (Svoboda, 1977; Muc, 1977), mean seasonal soil water content at 0-3 cm depth, and a one-day 24 h mean soil temperature at 5 cm depth (Courtin and Labine, 1977) for the four habitats.

	Crest	Slope	Transition	Meadow
Cover	80.5	92.4	100.0	98.0
Standing crop ($g\ m^{-2}$)	ca. 232	ca. 266	991.0	3207.0
Production ($g\ m^{-2}$)	ca. 10.8	ca. 12.3	53.4	230.7
Soil water (% oven dry wt)	11.8	24.3	190.0	746.4
Soil temperature (°C)	8.6	7.4	5.1	3.1

There are two possible explanations for the meadow's difference. First, the crest, slope and transition share an essentially common flora dominated by *Dryas integrifolia* (Svoboda, 1977), while the meadow is dominated by sedges (Muc, 1977). Second, the meadow was the coldest and wettest of the study areas (i.e. the soil was saturated - Addison, 1977a) (Table 9).

The extreme wetness of the meadow has several important consequences for nematodes. The meadow soil contains relatively little oxygen (Courtin and Labine, 1977), which diffuses slowly because the rate of oxygen diffusion is inversely related to soil water content. In addition, saturated soils may become anaerobic because bacteria use oxygen faster than it is replaced by diffusion (Nicholas, 1975). Finally, in soils which are generally anaerobic (e.g. bogs and marshes), bacteria may give rise to high concentrations of carbon dioxide, methane and hydrogen sulphide. Free-living soil nematodes are generally aerobic, and become quiescent when oxygen is limited or absent (Wallace, 1971). Nicholas (1975) reviewed the effects of anaerobiosis on nematodes. Oxygen deficiency seems to be a factor reducing the dispersal of nematodes in agricultural soils (Wallace, 1971) and, according to Nielsen (1949), may account for the lower densities of nematodes in saturated soils compared with well-drained soils.

The physical conditions of the meadow soil may affect nematode densities indirectly, through food supply.

Widden (1977) states that while the meadow had a large microbial population, this population is probably able to grow for only a short period in the spring, possibly due to oxygen limitation and low temperatures. In contrast, raised beach soils, which have lower microbial standing crop, are comparatively warm and well-aerated, thereby allowing micro-organisms to grow throughout the summer as long as mositure is not limiting. Widden suggests that the meadow has low microbial production, while the raised beach has high production.

Soil moisture content is an important factor in nematode movement. Small nematode generally use the surface tension forces of water films to obtain leverage for movement (Croll, 1970). In very wet habitats, where surface water films are inaccessible, nematodes are limited to swimming, which is an ineffective mode of locomotion for many soil living species.

It seems clear that the meadow, despite its greater plant biomass and production, is the least suitable nematode habitat of the four study sites because of its extreme wetness.

The seasonal variations in nematode densities within sites are more difficult to explain (Fig. 3). The low initial densities in 1972 may have been caused by the long preceding winter (the thaw in 1972 was nearly 4 weeks later than in 1973). Mortality during the shorter winter following 1972 appeared negligible, because initial 1973 densities were as high as late 1972 densities.

Initial 1972 densities were probably below habitat carrying capacities, which permitted the rapid increase to 1973 levels as the season progressed. With little winter mortality, initial 1973 densities were probably close to carrying capacity, and therefore changed little during the season.

Microhabitat variability was probably largely responsible for differences in densities between adjacent sampling dates.

3.4.3 Densities at 5 - 10 cm Soil Depth

When nematode densities at 5 - 10 cm depth (Table 7) are compared with densities at 0 - 5 cm depth, it is clear that most of the nematodes inhabit the top 5 cm of soil. When this concentration of nematodes is compared with the distribution of organic matter and temperature with soil depth, the reasons for the concentration seem clear. For example, on the crest organic matter comprised 3.7% of soil dry weight in the top 5 cm of soil, 1.4% at 5 - 10 cm depth, and 0.2% at 10 - 15 cm depth (Svoboda, 1974). Temperature likewise declined with increasing depth . For example, in the I.R.B. in 1973 accumulated 833 degree days above 0°C in the top 5 cm, 788 degree days at 5 - 10 cm depth, and 701 degree days at 10 - 15 cm depth (Courtin and Labine, 1977). The decline in organic matter and temperature from 5 - 10 cm depth to 10 - 15 cm depth presumably would be reflected by an even smaller number of nematodes at 10 - 15 cm depth than at 5 - 10 cm depth.

Nielsen (1949) studied nematode vertical distributions in several habitats and found that the largest percentage of the populations was generally at 0 - 1 cm soil depth, and that numbers decreased with depth to zero at about 20 cm depth. He concluded that a sampling depth of 0 - 10 cm will account for 80 - 100% of the fauna in most habitats.

In contrast to the situation in the top 5 cm, where densities increased from crest to transition, the proportion of nematodes at 5 - 10 cm depth decreased from crest to transition. Courtin and Labine's (1977) soil water data help explain this apparent anomally. Soil water in the top 3 cm of soil, expressed as percentage of soil dry weight, increased from crest (11.6%) through slope (34.7%) and transition (214.4%) to meadow (745.5%) in 1973. Soil water at 10 - 13 cm depth, which was consistently less than in the top 3 cm, also increased from crest (9.0%) to meadow (494.1%), although the slope had a slightly larger value (39.8%) than the transition (37.8%). The slope had the greatest proportion of soil water at 10 - 13 cm depth (53.4%), followed by the crest (43.7%), meadow (39.9%) and transition (15.0%). The relative dryness of the surface soil of the crest and slope is a function of height above the permafrost (and water table), high temperatures, exposure to wind, and open vegetation - which is less effective than closed vegetation in preventing evaporation. I believe that the combination of relatively dry habitat with relatively wet deeper soil accounts for the greater proportion of nematodes at 5 - 10 cm depth on the crest and slope than in the transition.

3.4.4 Densities in the Top 10 cm of Soil

In 1973 the four study sites averaged 480,000 m^{-2} more nematodes than in 1972 (a 12% increase) (Table 8). The 1973 summer was longer and warmer than in 1972 (833 degree-days compared to 397 degree-days at 0.5 cm depth on the I.R.B. - Courtin and Labine, 1977), resulting in increased plant production (ca. 10% - Bliss, 1977a), and probably a similar increase in micro-organism production.

I expect that few nematodes live below 10 cm depth, and the numbers presented in Table 8 are probably realistic estimates of all nematodes in the soil. These numbers can therefore be compared with estimates from other studies. Yeates (1972) compiled a list of published estimates of nematode densities, which range from 330,000 m^{-2} in a Danish grass field, to 29,800,000 m^{-2} in a German oak forest. Sohlenius (pers. comm.) compiled a more extensive list covering 20 temperate, tropical and alpine habitats, in which the densities range from 8,100 m^{-2} in a Puerto Rican rain forest (Coleman, 1970), to the German oak forest value previously cited by Yeates.

The average rank of my estimates lies above the midpoint of the estimates presented by Sohlenius. Data from other high latitude locations also show some high densities. Chernov (1975b) reported densities ranging from 800,000 m^{-2} in various tundra habitats on Taimyr Peninsular, U.S.S.R. Spaull (1973c) obtained densities of 250,000 -

1,970,000 m^{-2} on maritime Antarctic Signy Island. Alpine habitats may also have relatively high densities. For example, Wood (1971) obtained 3,180,000 nematodes m^{-2} in an Australian alpine herbfield. These values contrast with the low densities reported for tropical forests, which ranged from the 8,100 m^{-2} in the Puerto Rican rain forest mentioned above, to 41,000 m^{-2} in a rain forest in North Borneo (Kitazawa, 1971). The high nematode densities in high latitude/alpine habitats compared with tropical habitats complements my earlier conclusion (Chapter 2) that high latitude nematode faunas can be more diverse than tropical faunas. In Chapter 2 I suggested reasons why some high latitude habitats may be more favourable environments for nematodes than some habitats at lower latitudes.

3.4.5 Arctic Communities, and Predictions of Nematode Densities and Species Composition

Arctic tundra areas have been subdivided in several ways (e.g. Polunin, 1951; Andreev, 1966; Aleksandrova, 1970; Yurtsev, 1972; Bliss, 1975). I am using the zones 'Low Arctic' and 'High Arctic' as defined by Bliss (1975). According to Bliss, the Low Arctic encompasses and ends with the mainland of the continent, except for the southern end of Baffin Island. Low Arctic vegetation is charactersitically closed, and is dominated by sedge marshes and wet grassland-sedge areas, but includes areas of tussock-dwarf heath on rolling lands, lichen-dwarf heath shrubs on better-drained sites, and low shrub-dwarf heath with upland sedges on medium drained slopes nearer the tundra-forest border. The High Arctic, in terms of vegetation, characterizes all of the Arctic Archipelago, except for the southern part of Baffin Island. Bliss (op. cit.) divides the High Arctic into three main units: (1) tundra sedgelands and grasslands in low-lying areas; (2) Polar Semi-deserts of cushion plants or rush-grass steppes; and (3) Polar Deserts.

The southern islands, including Banks, Victoria and Prince of Wales, consist mainly of a mosaic of sedge-dominated lowlands and uplands, often only several metres higher in elevation, dominated by cushion plants. In the northern islands, tundra sedgelands and grasslands are restricted to coastal or near coastal lowlands of Devon (e.g. Truelove Lowland), Somerset, Cornwallis, Bathurst, Melville and Prince Patric islands, and to the fiord valleys of northern Baffin, Axel Heiberg and Ellesmere islands, and Greenland (Bliss, 1975). These lowlands, which occupy approximately 6% of the land area of the High Arctic, are related to the Low Arctic of the coastal plain of Alaska, areas in the Mackenzie Delta region, and areas on the Taimyr Peninsular, U.S.S.R., in terms of ecosystem structure and function, rather than to broad areas in the High Arctic (Bliss, 1977a).

Most of the High Arctic is Polar Semi-desert and Polar Desert. Polar Semi-desert, which covers 45% of the High Arctic land area (Bliss, 1977a), is comprised of cushion plant-moss/lichen communites, or herb-moss communities. The vegetation is characteristically open, with vascular plant cover averaging 5 to 20%, while mosses and lichens raise total cover to 50% in many areas. The cushion plant communities are typical of the well-drained low-lying uplands of Banks, Victoria and Prince of Wales islands, and the raised beach ridges within the coastal lowlands of Devon, Somerset, Bathurst, Cornwallis, Axel Heiberg and Ellesmere islands. Herb-moss communities are more characteristic of many areas of Melville and the Queen Elizabeth Islands (Bliss, 1975).

Polar Deserts, which account for 41% of the area of the High Arctic (Bliss, 1977a), have a depauperate flora

(5 - 10 vascular plant species in many areas) (Bliss, 1975). Vascular plant cover is about 1 - 5%, with lichens and mosses contributing an additional 1 - 10%. Patterned ground is widespread, and vascular plants are limited to the most favourable sites. Large areas have only occasional cryptogams and virtually no vascular plants.

Turning to my Truelove Lowland study sites, it is clear that the meadow represents a general community type that is characteristic of and widespread in the Low Arctic, but is of very limited occurrence in the High Arctic. On the other hand, the three raised beach sites represent a widespread High Arctic Polar Semi-desert community that is of limited occurrence in the Low Arctic. On the basis of the nematode density estimates obtained for the meadow and raised beach sites, I believe that large areas of the Low Arctic will prove to support substantially smaller populations of nematodes than does much of the High Arctic. Specifically, nematode densities in High Arctic Polar Semi-deserst may average 5 - 10 times greater than those in Low Arctic sedgelands. Data from the Low Arctic coastal plain of Alaska (Pt. Barrow) support my expectations. MacLean (1974) reported densities from various wet habitats at Pt. Barrow ranging from 50,000 m^{-2} to 740,000 m^{-2}.

While the Truelove Lowland meadows and raised beach study sites represent two distinct and general community types, each can be subdivided to offer additional insights into the distribution of nematode densities over large areas of Low and High Arctic. Muc (1977) distinguished three types of sedge meadow communities on Truelove Lowland - hummocky meadows (which I investigated), frost boil meadows, and wet meadows. Each of these meadow types is a widespread Low Arctic community (Polunin, 1948; Savile, 1964; Porsild, 1955; Johnson *et al.*, 1966; Beschel, 1970). Muc (*op. cit.*) found the greatest plant species diversity in hummocky meadows, which appear to offer a comparatively benign habitat that is intermediate between the other two meadow types. For example, the relatively dry frost boil meadows develop in unstable soil, and are presumably difficult for plants to establish in (plant standing crop and production was about half that of the other meadows - Muc, 1977). Wet meadows appear to be a flooded form of hummocky meadow, and their vegetation is restricted to plants tolerant of flooded conditions.

I expect both frost boil meadows and wet meadows to support lower nematode densities than hummocky meadows - the first because of soil instability, and the second because of extreme wetness. While I know of no data for frost boil meadows, MacLean (1974) reported nematode densities for wet meadows at Pt. Barrow ranging from 200,000 m^{-2} to 310,000 m^{-2}, compared with 740,000 m^{-2} for a mesic meadow. It is on the basis of these considerations that I suggested a 5 - 10 fold difference in densities between Low Arctic meadows and High Arctic Polar Semi-deserts, rather than the 2 - 3 fold difference I found between the hummocky meadow and the raised beach sites.

Diverging slightly from the theme of this section, it is noteworthy that the hummock and hollow physiography of hummocky meadows provides contrasting microhabitats which is reflected by the associated vegetation (Muc, 1977), and presumably by the nematode fauna. Compared to hummocks, hollows have shallower active layers, are colder, and have poorly aerated, supersaturated soils. Hollows therefore resemble wet meadows, and there is consequently a marked moisture gradient associated with the hummock/hollow microtopography. Bunnell _et al_. (1975) reported a ten-fold increase in nematode density along a similar moisture gradient associated with polygons, (i.e. from polygon basin to polygon rim). Evidently moisture gradients are a dominant factor affecting nematode densities in arctic regions, both at the microhabitat level, and in terms of broad community types.

So far in this discussion I have followed Bliss (1975, 1977a) in equating the combined crest, slope and transition sites with Polar Semi-desert. Svoboda (1977) provided information on the plant communities suggesting that the crest is comparable with productive Polar Deserts. In two sites on the Polar Desert plateau east of Truelove Lowland, vascular plant cover averaged 6.9%, compared with

7.4% on the crest of one Lowland raised beach (i.e. 'Phalarope'). Similarly, annual vascular plant production was 5.3 g m^{-2} in one Polar Desert site, compared with an average of 6.9 g m^{-2} for the crests of 11 raised beaches on the Lowland. The important contribution of cryptogams is less well-documented, but moss cover was 5.1% in one of the two Polar Desert sites, compared with 2.0% on the crest I studied. Keeping in mind that the crest I studied was the most productive of the 11 crests Svoboda investigated (i.e. vascular plant production was 15.0 g m^{-2}), and that nematode density in the 'average' crest is probably substantially lower than my measured density of 2,795,000 m^{-2} (average value from Table 8), productive Polar Deserts conceivably may support nematode densities in the order of 1,000,000 m^{-2}. In the large areas of Polar Desert where net vascular plant production possibly averages only 0.5 g m^{-2} (Svoboda, 1977), nematode densities may be reduced to 1/10 of the above estimate. If these predictions prove correct, High Arctic Polar Deserts and some Low Arctic communities (e.g. wet meadows) support similar densities of nematodes.

I mentioned in Chapter 2.3.2.5, that nematodes are better equipped than many invertebrates to utilize areas of low/uncertain production. While Polar Deserts are resource poor, these resources have patchy distributions, with relatively high local concentrations. Nematodes are likely to show a similar pattern of densities. I base this expectation on the widespread occurrence of patterned ground in Polar Deserts, which is an important factor in the distribution of plants. Most plants, and especially mosses, are concentrated in the shallow troughs of polygons, or between or under frost shattered rock fragments (Muc and Bliss, 1977). In water-deficient Polar Deserts the low-lying, sheltered troughs are relatively moist, and consequently are a favoured microhabitat for both plants and invertebrates. This situation contrasts with that in wet hummocky meadows, in which the elevated dry end of the moisture gradient favours most terrestrial organisms, including nematodes.

In concluding, I wish to make clear that the four study sites do not represent all arctic communities. For example, my studies are not applicable to dwarf shrub heath communities which, while present on Truelove Lowland, are characteristic of the Low Arctic (Bliss _et al_., 1977). Likewise my studies do not apply to the relatively dry graminoid-moss meadows of better-drained uplands (Muc and Bliss, 1977; Bliss _et al_., 1977). Another distinctive community not represented by my study sites is the coastal salt marsh, which is found through much of the Low and High Arctic (Muc and Bliss, 1977). However, despite these omissions, my studies provide information of nematode densities that is applicable to diverse communities covering most of the High Arctic, and also to large areas of the Low Arctic.

I did not determine the distribution and abundance of nematode taxa in the study sites. However, there is sufficient published information on species moisture preferences (e.g. Nielsen, 1948, 1949) to offer a basis for speculation on site taxonomic composition, and thereby the composition in the communities each site represents. For example, in the wet habitats (e.g. hollows of hummocky meadows, and wet meadows), species of the genera *Chromadora*, *Monhystera* and *Dorylaimus* are likely to be among the dominant nematodes. Many species of the first two genera live in freshwater, and appear to be restricted to this environment. The nematode fauna of very wet terrestrial environments probably resembles the flora of wet meadows in being reduced in diversity, because of the limited number of species that tolerate these conditions (*cf*. Muc, 1977).

A majority of soil living nematodes appears to favour moderately wet to 'normal' soils (Nielsen, 1949). Species of the genera *Dorylaimus*, *Mononchus*, *Teratocephalus*, *Achromadora*, *Rhabdolaimus*, *Aphelenchoides*, *Alaimus*, *Prismatolaimus*, *Cephalobus*, *Bunonema*, *Wilsonema*, *Acrobeles*, *Tylencholaimus*, *Tylenchus* and *Plectus*, among others, are likely to be important in these intermediate conditions. Furthermore, species characteristic of very wet and very dry habitats may overlap in such environments. Of my study sites, the transition and slope (i.e. Polar Semi-desert) probably best represent 'intermediate' soil conditions, and

I expect high species diversity to complement the high densities I found in these sites.

Relatively few species appear consistently abundant in very dry habitats. Nielsen (1949) lists three genera, Aphelenchoides, Tylenchus and Plectus, as important contributors to the faunas of some dry habitats. Species of the genus Plectus, in particular, are notable for their very wide ecological range, the same species in some cases being found from the wettest to the driest environments. Plectids are also notable for their frequent association with mosses and lichens which, in view of the importance of these plants in many arctic communities, is one explanation of the abundance of plectids in high latitudes (and high altitudes). I expect species of the genus Tylenchus and, more particularly, Plectus to be major contributors to the reduced faunas of Polar Deserts.

Nielsen (1949) considers soil water conditions a major factor in the distribution of soil living nematodes. Regardless of the nature of the habitat, the activity of nematodes depends on the presence of free water. The species composition of the fauna is modified by the degree of constancy of the water, the richest fauna being found in permanent water films and columns. In order to exist in intermittently wet environments, the animals must be able to survive these periods of drought. This ability is either absent, or poorly developed, in typical freshwater forms (e.g. Chromadora, Monhystera), but is well-developed in typical moss-living species, most notably, some species of Plectus (Nielsen, op. cit.).

To recapitulate, the declining moisture gradient from wet meadows (or lakes) to Polar Deserts, is paralleled by a decline in constancy of soil moisture, which should be reflected in nematode faunas that contain progressively increasing proportions of drought-resistant species. Because the study sites, and therefore the arctic communities they represent, lie along a well-defined gradient based on a limited number of edaphic factors, the associated nematode faunas probably can be distinguished and defined using community ordination techniques such as those used by Johnson et al. (1972, 1973). These techniques are likely to be more effective in defining these arctic nematode faunas than in separating many lower latitude faunas because, as Johnson et al. (1973) found, in closely related temperate communities no single factor had a dominating influence throughout all the communities.

Chapter 4

NEMATODE STANDING CROPS

4.1 Introduction

In this chapter I provide estimates of mean annual nematode standing crop for the four study areas. These estimates are expressed in mg dry weight m^{-2}, and in calories m^{-2}. I have compared the dry weight estimates with similar information for other high latitudes, temperate and tropical nematode faunas. I have also compared nematode standing crops expressed in calories with equivalent information for the other important invertebrate groups in the Truelove Lowland study sites. On the basis of the relative and absolute contributions of nematodes and other taxa to total invertebrate standing crop in the study areas, I have predicted their contributions to invertebrate standing crop in some widespread arctic communities.

My standing crop estimates are based on a study of seasonal and intersite distributions of mean individual nematode dry weights. These field estimates of mean weight serve as one standard for testing and refining the output of the Ryan and Whitfield production model (Ryan, 1977b), which I used to calculate nematode production (Chapter 7), and whose output includes an estimate of standing crop. The seasonal distribution of mean weights also offers insight into the distribution of age classes in time.

4.2 Methods

I took a representative sample of nematodes from a randomly selected soil sample from each study site on five equidistant dates spanning the 1973 season (i.e. 18 June, 6 July, 27 July, 17 August, 7 September). I weighed the samples on a Cahn G2 Electrobalance accurate to 0.05 ug, after drying for 24 hr at 80°C with calcium chloride. For each of the 20 samples I divided the total dry weight by the number of nematodes in the sample in order to obtain the mean dry weight in ug individual^{-1}. The number of nematodes in the samples ranged from 126 to 561 individuals.

I used the two-way anova without replication (Sokal and Rohlf, 1969) to test for differences in weight in time within study sites, and for differences in weight between study sites.

The mean dry weight individual^{-1} nematode determined by the above procedures I combined with the density information presented in chapter 3 to estimate mean annual standing crops in the study sites.

I converted published nematode standing crops expressed in live weight to dry weight according to information provided by Yeates (1972), who found that nematode dry weight is 58.5% of fresh weight. I also used information provided by Yeates on the caloric content of nematode tissue to express my standing crop estimates in calories. Yeates obtained a whole body calorific value of 4.285 cal mg^{-1} ashfree substrate, and 3.679 cal mg^{-1} ash-included substrate for Plectus sp. and Poikilolaimus sp. I used the ash-included value for my standing crop calculations.

I drew on information on invertebrate standing crops obtained by Ryan (1977a, 1977c) for comparison with my nematode standing crops in the study sites.

4.3 Results

The mean dry weight individual^{-1} nematode was 0.4297 ± 0.1808 ug (Table 10). There was no difference in weight between dates, or between study sites, at the 95% confidence level.

Mean individual dry weights for nematode faunas of other high latitude/alpine environments varied between 0.0533 ug and 1.1946 ug, while the weights of lower latitude faunas ranged from 0.1170 ug to 2.7086 ug (Table 11).

On Truelove Lowland the mean seasonal standing crop of nematodes in gm dry weight m^{-2} in the top 10 cm of soil ranged from 0.5589 gm (meadow) to 2.0221 gm (transition) in 1972, and from 0.6722 mg (meadow) to 2.0016 mg (slope) in 1973 (Table 12). The same standing crops expressed in calories m^{-2} were 2056 and 7439 calories in 1972, and 2473 and 7364 calories in 1973.

Mean seasonal nematode standing crops for other high latitude/alpine faunas ranged from 0.0120 gms to 4.8261 gms dry weight (Table 11). The range for lower latitude faunas was 0.0047-10.4130 gms.

Nematodes dominated invertebrate standing crop on the raised beach with 6661 calories m^{-2}, or 77% of the total (Table 13). The Enchytraeidae were the next most important group, accounting for 924 calories (11%). The contribution of the other groups to standing crop was relatively unimportant. In the meadow nematodes contributed 31% of invertebrate standing crop. The Enchytraeidae and Diptera were the other dominant invertebrates in the meadow, with 3030 calories (46%) and 851 calories (13%) respectively.

Table 10. Mean dry weight in μg per individual nematode in the four habitats on different dates in 1973. Each weight is the mean of 126-561 individuals.

	18/6/73	6/7/73	27/7/73	17/8/73	7/9/73
Crest	0.6457	0.5284	0.3918	0.2917	0.3654
Slope	0.1392	0.2564	0.6349	0.4091	0.7391
Trans.	0.2582	0.2138	0.2541	0.3701	0.5762
Meadow	0.6135	0.4272	0.7540	0.3000	0.4242

Grand mean = 0.4297 ± 0.1808

Table 11. Mean individual dry weight in ug, and seasonal mean standing crop in gm dry weight m^{-2}, of some high latitude, temperate and tropical nematode faunas. The mean dry weights marked with an '*', and the associated standing crops, have been converted from live weights according to Yeates (1972).

Habitat	Ind. biomass ug dry wt	Standing crop gm dry wt m^{-2}	Author
Pt. Barrow, Alaska	0.1000	0.0120-0.1120	Bunnell *et al.*,1975.
Signy Island. Antarctica	0.1167-1.1946*	0.0918-4.8261	Spaull, 1973d.
Stordalen, Sweden	0.0533	0.2132	Lagerlöf *et al.*,1975.
Moor House, England	0.1435*	0.2797-0.4394	Banage, 1963.
Tareya, Russia	0.3510-0.5400*	0.4563-4.2120	Chernov, 1975.
Tropical rain forest, Puerto Rico	0.2404-0.5780*	0.0047-0.0059	Coleman, 1970.

Table 11. Continued.

Habitat	Ind. biomass ug dry wt	Standing crop gm dry wt m^{-2}	Author
Tropical rain forest, North Borneo	2.3400*	0.0234	Kitazawa, 1971.
Beech woodland, England	0.1170*	0.0436	Phillipson *et al*., 1977.
Cool-temperate deciduous forest, Japan	0.9360*	0.1170	Kitazawa, 1967.
Beech forest, Denmark	0.1509	0.2165	Yeates, 1972.
Alpine herb-field, Australia	0.1714*	0.4388	Wood, 1971.
Mixed fen, England	0.2943*	0.4434	Yeates, 1971.
Heath moor, Denmark	1.7726*	0.5850	Nielsen, 1949.

Table 11. Continued.

Habitat	Ind. biomass ug dry wt	Standing crop gm dry wt m^{-2}	Author
Dry sclerophyll forest, Australia	0.1281*	0.9536	Wood, 1971.
Old fields, South Carolina, U.S.A.	2.7086*	1.0238	Coleman, 1971.
Wet sclerophyll forest, Australia	0.2018*	1.1993	Wood, 1971.
Beech forest, Germany	0.1983*	2.3985	Volz, 1951.
Spruce forest, Denmark	1.5485*	2.6325	Nielsen, 1949.
Natural grassland, Canada	0.3600	3.0356	Willard, 1973.
Oak forest, Germany	0.2984*	8.8920	Volz, 1951.
Grass field, Denmark	0.5207*	10.4130	Nielsen, 1949.

Table 12. Mean seasonal standing crop of nematodes in gm dry weight m^{-2} and cal m^{-2} in the top 10 cm of soil.

	1972		1973	
	gm	cal	gm	cal
Slope	1.0989	4043	1.5182	5585
Crest	1.6769	6169	2.0016	7364
Transition	2.0221	7439	1.9900	7321
Meadow	0.5589	2056	0.6722	2473
Mean	1.3392	4927	1.5455	5686

Table 13. The 1972 mean seasonal nematode standing crop, expressed in calories m^{-2}, for the raised beach and meadow, compared with similar information for other important invertebrate taxa (calculated from Ryan, 1977a)(nematode raised beach value = mean of the crest, slope & transition values weighted in the ratio 1:1:4 according to Svoboda, 1977).

	Raised beach		Meadow	
Taxa	Cal m^{-2}	%	Cal m^{-2}	%
Nematoda	6661	77.2	2056	31.3
Enchytraeidae	924	10.7	3030	46.1
Collembola	561	6.5	247	3.8
Acarina	314	3.6	220	3.3
Diptera	135	1.6	851	12.9
Crustacea	0	0	161	2.4
Tardigrada	30	0.4	12	0.2
Total	8625		6577	

4.4 Discussion

4.4.1 Nematode Standing Crops in the Four Study Areas

On the basis of the two-way anova without replication, I used the grand mean of the individual dry weights to calculate standing crop in each of the study sites. The two-way anova with replication would be a more critical test for trends in weight, but would require a five-fold increase in the experimental work required and, in view of the variation in my data, I feel would lead to the same conclusions I made on the basis of the two-way anova without replication. The main consequence of my decision is that the distribution of nematode biomass is strictly proportional to the distribution of densities.

An important implication of my finding that weight is constant with time is that recruitment to the nematode population is evenly distributed throughout the growing season. For example, a significantly lower mean individual biomass at some period probably indicates a high recruitment of juveniles during that period. Nielsen (1961) suggested that in nematodes (which have several overlapping generations per year) there will be drift towards "stable age distribution" (Andrewartha and Birch, 1954), and that there will therefore be stabilization of mean body weight. Phillipson *et al*. (1977) concluded that their data generally supported this expectation of constant body weight, with underlying constant recruitment, in the nematode populations they studied.

The mean individual dry weight I obtained is similar to the mean of 0.36 ug reported by Willard (1973) for the fauna of a natural grassland. Willard used the same method as I to obtain his weights. It is difficult to compare these dry weights, and the derived field estimates of standing crop, with data from other studies because nematode biomass has usually been reported as live weight, and it is unclear how wet weight is related to dry weight. For example, Yeates (1972) determined that the average dry weight of nematodes is 58.5% of live weight, with live weight being determined by the volumetric method according to Andrassy (1956). However, Andrassy (*op*. *cit*.) gives a dry matter content of 10% for *Aphelenchus* *avenae*, while Evans (1970) and de Soyza (1973) reported dry matter content of 31% and 20% respectively for this species. In order to make interstudy comparisons, Willard (1973) converted live weight to dry weight using Yeates' value of 58.5%. I followed Willard's procedure in my study, but I emphasize that the published range of conversion factors makes the accuracy of Yeates' value uncertain - if there is a major error associated with his value, the resulting dry weights, and derived standing crops, are probably over-estimated.

In the several tundra communities studied by Chernov (1975) (e.g. *Dryas* sedge-moss hummocky meadows, herb *Dryas* stand, herb grass stand), mean dry weights, converted from wet weights according to Yeates (1972), ranged from 0.3510 ug to 0.5400 ug. These values are interchangeable with my estimate. Dry weights from other tundra sites are lower. Bunnell *et al*. (1975) used a mean dry weight of 0.1 ug, but the origin of this value is uncertain. Lagerlöf *et al*. (1975) determined a mean weight of 0.0533 ug, using live weight information from Banage (1963) and Andrassy (1956), which they converted according to de Soyza (1973). Spaull (1973c) also used Andrassy's procedures to obtain live weights which, converted by me according to Yeates, gave mean dry weights ranging from 0.0675 to 0.7000 ug for the communities Spaull studied.

In view of the diverse origins of these data, and of the information on temperate and tropical faunas, it is difficult to be confident about conclusions drawn from comparisons made between them. However, I am confident that the average weight of the nematodes of Truelove Lowland, and probably of Tareya (Chernov, 1975) and Signy Island (Spaull, 1973c) as well, is higher than for many lower latitude nematode faunas. Consequently, the standing crops of these faunas are relatively larger compared with lower latitude faunas than would be expected on the basis of densities alone. The main reason for these high average weights is the numerical importance of species of the genera Plectus, Eudorylaimus and Dorylaimus, which generally are large nematodes (e.g. Plectus parientinus adults weighed 3.01-3.85 ug, Eudorylaimus spp. adults weighed 1.66-17.33 ug - Spaull, 1973c). Of course, any fauna, whether high latitude or low, in which these genera are numerically important will have high average weight (e.g. Nielsen, 1949).

4.4.2 Arctic Communities, and Predictions of Nematode Standing Crops, and Relative Contribution to Invertebrate Standing Crops

Because mean individual nematode biomass was the same for the four study sites, the arctic communities represented by the study sites will have nematode standing crops that are proportional to the nematode densities they support. For example, drawing on the rationale and predicted densities I offered in Chapter 3.4.5, Low Arctic meadows probably support standing crops in the order of 0.2-0.4 gm dry weight m^{-2}, compared with approximately 2.0 gm I obtained in the Polar Semi-desert. Similarly, productive Polar Desert may support 0.5 gm of nematode standing crop, and unproductive Polar Desert about 0.05 gm.

As a noteworthy aside, my predicted nematode standing crop for unproductive Polar Desert is higher than the standing crops of the two tropical rain forests I listed, and is similar to that of a beech woodland in England (Table 11). Productive Polar Desert is even more impressive - my predicted value is larger than half of the listed tropical and temperate standing crops. Assuming these expectations are valid, they support my thesis that High Arctic environments are more favourable for soil nematodes than are many lower latitude environments.

Useful predictions can also be made concerning the relative contribution of nematodes to invertebrate standing crop in arctic communities. For example, although nematodes contributed significantly to invertebrate standing crop in the hummocky meadow, aquatic invertebrates (e.g. Enchytraeidae, Diptera, Crustacea) were the dominant contributors (i.e. 61%). Bearing in mind the lower nematode densities and standing crops I predicted for Low Arctic wet meadows, I expect that in large areas of Low Arctic nematodes contribute a smaller proportion of invertebrate standing crop than the 31% I recorded in the mesic hummocky meadow. For example, nematodes contributed an average of 3% of standing crop of the major invertebrate groups involved in decomposition processes in several hydric habitats at Pt. Barrow, Alaska (Bunnell _et al_., 1975).

On the basis of the overwhelming contribution of nematodes to invertebrate standing crop on the raised beach (i.e. 77%), I expect nematodes to dominate invertebrate standing crop in High Arctic Polar Semi-deserts and Polar Deserts. One reason for the dominance of nematodes in these typical High Arctic communities is the marked decline or loss of several groups that are important contributors to invertebrate standing crop in wet environments, including the Enchytraeidae, Chironomidae and Crustacea. These groups I consider "typical" Low Arctic invertebrates, which occur in the High Arctic as a result of "historical accident" that has placed small areas of wet Low Arctic in the dry High Arctic.

Apart from nematodes, several groups, including Collembola and Acarina (Addison, 1977b; Ryan, 1977a), increase from meadow to raised beach. These I consider "typical" High Arctic invertebrates. However, I expect the relative contribution of nematodes to invertebrate standing crop increases from Polar Semi-desert to Polar Desert, because nematodes are probably least committed to living closely associated with the very sparse vascular plants (cf. Addison, 1977b), can relatively easily avoid extreme conditions at the soil surface by living deeper in the soil (Chapter 3.4.3), and have high tolerance of dry conditions. Data for the Acarina support my expectations. Combining Acarina density information (Addison, pers. comm.) with biomass data (Ryan, 1977a), I estimated that in 1972 mites contributed 0.0852 gm to invertebrate biomass in the transition zone, and only 0.0255 gm on the combined slope and crest. By comparison, nematodes accounted for 2.0221 gm in the transition, and 1.3879 gm on the combined slope and crest. Collembola do not so clearly support my expectations. Addison (1977b) estimated Collembola standing crop on the Plateau (Polar Desert) to be 0.0053 gm dry weight m^{-2} in 1973, compared with my nematode estimate of about 0.2 gm.

By comparison, on the combined slope and crest Collembola accounted for 0.0536 gm in 1973, while nematodes contributed 1.7599 gm. Collembola, like nematodes, appear able to move deeper into the soil as surface conditions deteriorate (Addison, op. cit.). Consequently, I expect Collembola also to increase in relative contribution to invertebrate standing crop as one progresses from Polar Semi-desert to Polar Desert.

Other terrestrial environments in which nematodes probably contribute a large proportion of invertebrate standing crop include beaches (e.g. sand dunes - Yeates, 1968), hot deserts (e.g. Crawford, 1979) and alpine habitats. The relatively harsh conditions at the soil surface in these environments probably selectively reduce invertebrates that cannot readily move and live below the surface.

Finally, the distribution of total invertebrate biomass among the study sites may indicate the relative amount of invertebrate standing crop to be expected in the major arctic communities. Invertebrate standing crop of the raised beach was 25% larger than that of the meadow (Table 13). Bearing in mind that the transition and slope contribute a larger proportion of raised beach invertebrate standing crop than does the crest, these data raise the possibility that High Arctic Polar Semi-deserts support standing crops that are as large as, or larger than those of

Low Arctic wet meadows. Furthermore, productive Polar Deserts may come close to meadows in biomass supported. For example, in 1972 the crest had 4043 calories m^{-2} of nematode tissue, compared with the meadow's 6577 calories of invertebrate tissue. Of course, the relatively high invertebrate biomass I expect in High Arctic communities partly reflects the large nematode biomass in these communities. Muc (1977) offers another partial explanation for my expectations in noting that flooding "... led to a reduction in (plant) species composition and a more uniform distribution of plants tolerant of flooded conditions." He found that mean seasonal vascular plant standing crop was lower in wet meadows than in drier hummocky meadows.

Chapter 5

GROWTH, REPRODUCTION AND POPULATION GROWTH OF *CHILOPLACUS* SP.

5.1 Introduction

I know of no information on growth, reproduction and population growth for High Arctic free-living soil nematodes at the temperatures they commonly encounter. In this chapter I present this information for an undescribed species of the genus *Chiloplacus* (Family Cephalobidae). This genus is represented by at least three species at Lake Hazen, Ellesmere Island, in the Canadian High Arctic (Mulvey, 1963). These are generally medium-sized nematodes of a little under 1.0 mm length as adults. Most of the species have been found in decaying plant material or in soil. According to Goodey and Goodey (1963) they are probably saprophagus or microbivorous feeders.

I studied in detail individual growth rate and reproductive rate at 10°C (Truelove Lowland soil temepratures reached 17°C at 5 cm depth - Courtin and Labine, 1977), and I determined population growth rates at temperatures ranging from 0°C to 25°C. I chose to include growth rate response at high temperatures to permit direct comparison with similar information for temperate and tropical nematodes. In reviewing research on adaptation of invertebrates to life in cold environments, it became clear to me that there are few studies which compare the performances of animals from high and low latitudes under similar conditions (cf. Scholander et al., 1953). The population growth rate studies also illustrate the effect of temperature on instrinsic rate of increase (r), which I believe has not previously been done for a free-living soil nematode.

An important function of my studies of Chiloplacus sp. was to provide information required by the Ryan and Whitfield production model (Ryan, 1977a) to estimate nematode production. I am treating Chiloplacus sp. as a 'representative' arctic nematode, and these data supercede information I used to obtain earlier production estimates (Procter, 1977a). Pertinent information includes weight range, duration of larval and adult stages, and fecundity. These studies also provide an independent estimate of cohort duration, which is part of the production model's output, thereby permitting partial testing of the model's performance.

Several of the above experiments presented serious technical problems. Weighing the small numbers of nematodes involved in some experiments, and aging specimens was difficult. To circumvent these problems I performed several additional experiments to obtain functions allowing me to estimate weight and age from length information, length being quick and easy to determine.

5.2 Methods

5.2.1 Conversion Factors

5.2.1.1 Length-Weight Relationship

The range of lengths encompassed by newly hatched and adult nematodes (from $\hat{=}$ 0.24 mm to 1.32 mm) was subdivided into 28 units of 0.04 mm length. I accumulated several individuals at each length (e.g. 470 ind. of $\hat{=}$ 0.24 mm, and 10 ind. of 1.28-1.32 mm), and determined their combined and mean dry weights according to the methods in Chapter 4.2. I then plotted logarithmically the mean dry weight against length, and obtained a regression equation according to Sokal and Rohlf (1969). This equation was used to estimate dry weight from observed length.

5.2.1.2 Length-Age Relationship at 10°C

I used the logistic equation describing the growth curve of Chiloplacus sp. at 10°C (Section 5.2.2) to convert dry weight to age, according to the function

$W = \frac{0.5085}{1 + e^{-0.1725\,(t-23.7)}}$ (e.g. Ricklefs, 1967). Because I previously related dry weight to length with the regression equation (Section 5.2.1.1), the two equations together allow age to be estimated from length at 10°C.

5.2.2 Growth of Chiloplacus sp. at 10°C

I carried out the growth experiments in 90 mm diameter X 15 mm high petri dishes. A colony of the fungus Phoma sp. (Widden, 1977) was established in each dish as food for the nematodes, using Difco Bacto-agar containing domestic vegetable juice (V8) as the fungal growth medium. Each dish was inoculated with 40 newly hatched (i.e. <24 hr old) second stage larvae, which were drawn from a colony maintained at 10°C. Forty-five dishes were prepared in this manner, then were divided into 15 sets of 3 replicates and placed in a Precision Scientific Co. Freas Low Temperature Incubator (Model 815) at 10.0 ± 0.3°C. The dishes were kept in a darkened box to avoid possible influence of light on development.

I sacrificed one set of replicates every fourth day following initiation of the experiment until day 60, when the last replicates were taken. The nematodes were extracted, killed, counted, and the length of each nematode recorded. The first appearance of eggs and juvenile nematodes was also noted. I determined the mean length individual nematode^{-1} replicate^{-1}, and converted these data to dry weight according to the regression equation $\log W = -0.4062 + 2.6536 \log L$ (Section 5.3.1). The mean weight of each set of converted replicates I used as my measure of growth.

With the growth data expressed as dry weight, I fitted the logistic, Gompertz and von Bertalanffy growth equations to the growth curve according to procedures given by Ricklefs (1967). Because the logistic equation gave the best fit, I used it to characterize the growth curve.

5.2.3 Reproduction of Chiloplacus sp. at 10°C

5.2.3.1 Duration of Egg Stage, and Hatching Success

One hundred newly laid eggs ($<$24 hr old) obtained from adults reared at 10°C were placed in each of five 68 mm diameter X 18 mm high glass dishes containing distilled water. Each dish was covered with a petri dish lid and placed in a Freas Low Temperature Incubator at 10.0±0.3°C. The dishes were checked on alternate days for newly hatched larvae, which were removed, counted, and time of hatching recorded. I continued this procedure until no further eggs hatched.

5.2.3.2 Number of Eggs laid per Female, Age-specific Fecundity Rates, and Intrinsic Rate of Natural Increase

The reproduction experiments, like the growth studies (i.e. Section 5.2.2) were conducted in petri dishes containing colonies of the fungus Phoma sp. However, for the reproduction experiments I innoculated each dish with one pre-reproductive individual, which I drew from a culture maintained at 10°C. I established six replicates, which I placed in a darkened box in a Freas Incubator at 10.0±0.3°C. Every seventh day following initiation of the experiments, I extracted and counted the eggs and nematodes, and measured the juvenile nematodes. The founding adults

I returned to the cultures after each extraction. I followed this procedure until no further eggs or nematodes occurred in the cultures (i.e. 77 days after the experiments started). I also recorded time of disappearance of each founding adult. Because the age span of the extracted juvenile nematodes was at least seven days, due to the seven-day sampling interval, I aged them using the length-age relationship outlined in Section 5.2.1.2. The extracted eggs had a similar range in age but, because I did not establish a method of aging them, I arbitrarily distributed them evenly among the preceding seven days.

Because the above procedures did not permit direct observation of eggs laid female^{-1}, I obtained this information indirectly. For example, I estimated the number of eggs laid to produce the observed number of juveniles by increasing the observed number of juveniles in proportion to the percentage hatching success. Similarly, to obtain the number of juveniles hatched, I reduced the observed number of eggs in proportion to the percentage hatching success, and combined this figure with the observed number of juveniles.

I determined (1) age-specific fecundity rates for the egg-laying period; (2) net reproductive rate 'R_o'; (3) intrinsic rate of increase 'r'; (4) mean length of a generation 'T'; (5) the contribution of each age group to the value of 'r'; (6) stable age distribution, and (7) birth-rate and death-rate, according to procedures given by Birch (1948).

5.2.4 Population growth of Chiloplacus sp. at various temperatures

I conducted the population growth studies at 0°, 2°, 5°, 10°, 15°, 20° and 25°C. These experiments also took place in petri dishes containing the fungus Phoma sp. However, for the population studies I inoculated each dish with five gravid females obtained from colonies maintained at the experimental temperatures. I established six sets of three replicates at 0°, 2° and 5°C, and four sets of three replicates at 10°, 15° 20° and 25°C. The cultures were maintained in Freas incubators at the appropriate temperatures. Single sets of replicates were sacrificed at 28-day intervals at 0°, 2°, 5° and 10°C, and at 14-day intervals at 15°, 20° and 25°C. The nematodes were extracted, killed and counted. Because the numbers of nematodes often became very large as the experiments progressed, I subsampled to facilitate counting (cf. Chapter 3.2).

I fitted several descriptive functions to the growth data, including the logistic, Gompertz and von Bertalanffy growth equations (Ricklefs, 1967), and I also tested for geometric progression in these data (Williams, 1961). Because the exponential growth expression, $r = \frac{\log_e N(t) - \log_e N(0)}{t}$, best described population growth, I used this function to determine the rate of population growth at all temperatures.

To determine the lowest temperature at which population growth occurs, I plotted rate of population increase 'r' at each temperature against temperature, and obtained a regression equation according to Sokal and Rohlf (1969). The critical temperature I obtained in this manner I used as the base on which to express generation time and cohort duration in degree-days.

5.3 Results

5.3.1 Conversion factors

The relationship between body weight, W, and length, L, is represented by the equation:

$$\log W = -0.4062 + 2.6526 \log L,$$

where W is in ug dry wt, L is in mm, -0.4062 (log weight of a 1 mm individual) is the intercept, and 2.6526 is the slope of the log-log plot of weight versus length (Figure 4). The 95% confidence limits for -0.4062 are -0.4384 and -0.3739. The regression coefficient is significant at $p = 0.01$, and the 95% confidence limits are 2.5280 and 2.7772, while the coefficient of determination, $r^2 = 0.9843$.

According to the length/age equivalents presented in Table 14, a 0.24 mm long individual is 0.3 days old, while a 1.0 mm individual is 30.8 days old. The 0.04 mm length interval is $\simeq$ 2 days in age.

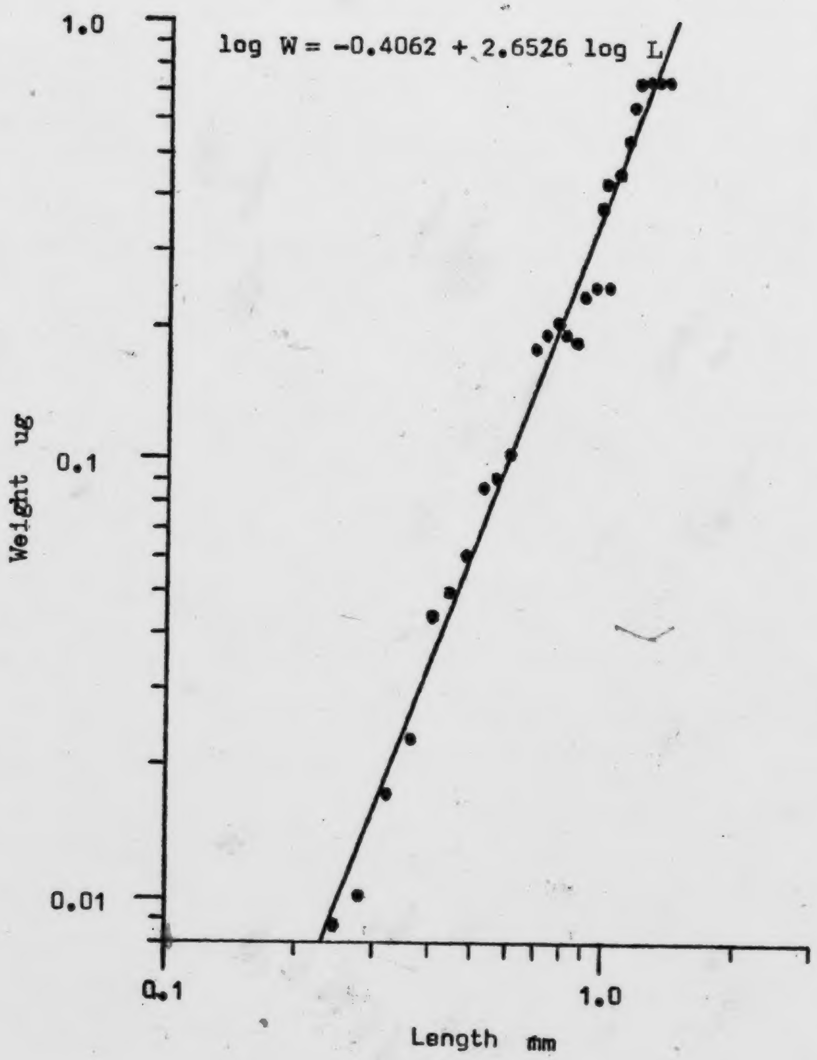


Fig. 4. Weight as a function of length for Chiloplacus sp.

Table 14. Length/age equivalents based on the equations:

$$\log W = -0.4062 + 2.6526 \log L$$

(log weight regressed on log length); and

$$W = \frac{0.5085}{1 + e^{-0.1725(t-23.7)}}$$

(logistic equation relating weight to age).

Length (L) mm	Weight (W) ug	Logistic conversion factors	Age days
0.24	0.0089	-1.0070	0.3
0.28	0.0134	-0.9024	2.8
0.32	0.0191	-0.8109	4.9
0.36	0.0261	-0.7292	6.8
0.40	0.0345	-0.6551	8.5
0.44	0.0445	-0.5861	10.1
0.48	0.0560	-0.5224	11.6
0.52	0.0693	-0.4616	13.0
0.56	0.0843	-0.4040	14.3
0.60	0.1013	-0.3478	15.6
0.64	0.1202	-0.2932	16.9
0.68	0.1411	-0.2392	18.2
0.72	0.1642	-0.1851	19.4
0.76	0.1895	-0.1302	20.7
0.80	0.2172	-0.0734	22.0
0.84	0.2472	-0.0139	23.4
0.88	0.2796	0.0500	24.9
0.92	0.3146	0.1210	26.5
0.96	0.3522	0.2031	28.4
1.00	0.3925	0.3047	30.8
1.04	0.4354	0.4461	34.1
1.08	0.4813	0.7183	40.4

5.3.2 Growth of Chiloplacus sp. at 10°C

The growth curve of Chiloplacus sp., expressed in weight, was sigmoid in form (Figure 5). Mean hatching weight was 0.0084 ug dry weight, and the maximum adult weight was 0.5260 ug (Table 15). The first eggs, weighing 0.0092 ug, were laid 26 ± 2 days after hatching, by individuals weighing approximately 0.3 ug. The first juveniles appeared 38 ± 2 days after their parents hatched.

The growth of Chiloplacus sp. is described by the equation:

$$W = \frac{0.5085}{1 + e^{-0.1725(t-23.7)}}$$

where W is dry weight in ug, 0.5085 is the asymptote in ug dry weight, 0.1725 is a constant which is proportional to overall growth rate, t is time in days from hatching, and 23.7 is time in days from hatching to the point of inflection of the growth curve.

The logistic conversion factors for the growth curve are plotted against time in Figure 6, and the growth curve with the weight data expressed as percentages of the asymptote, is shown in Figure 7.

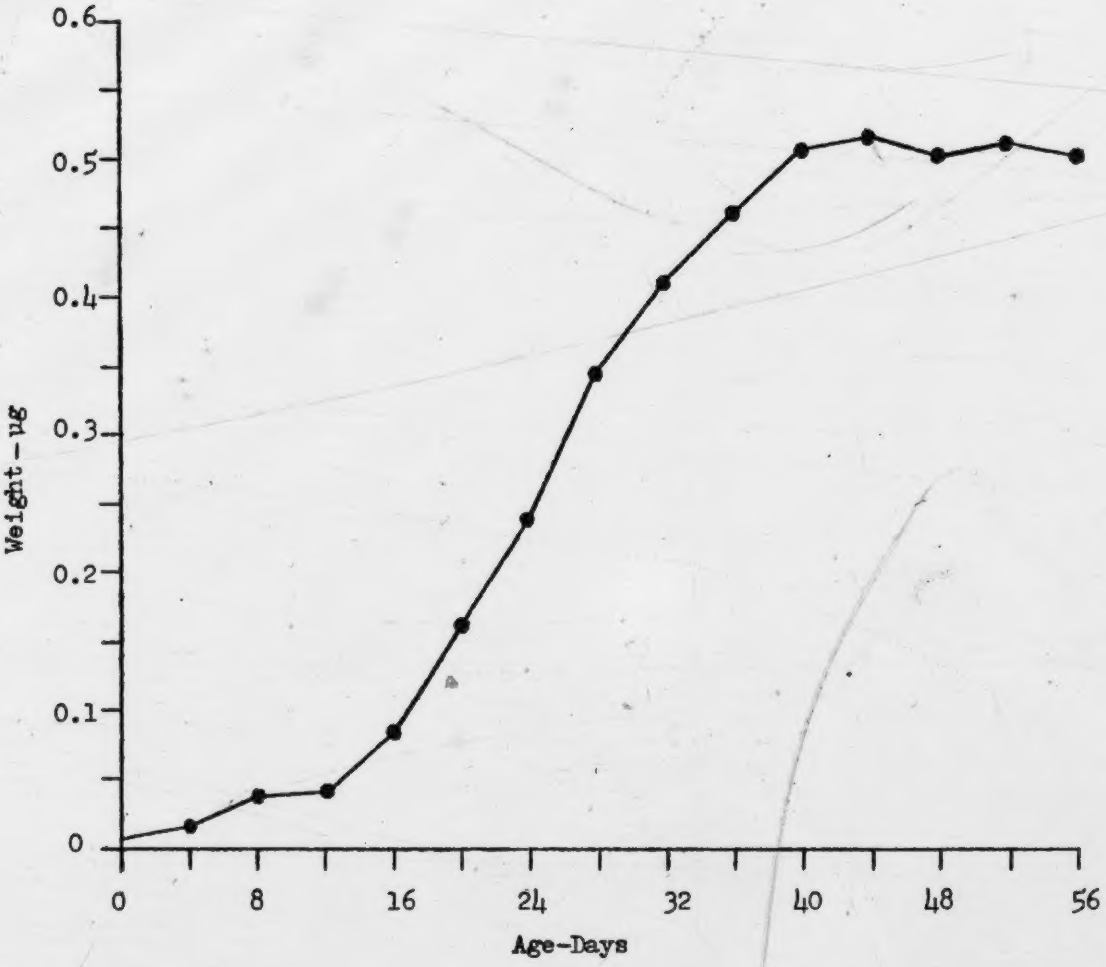


Fig. 5. The growth curve of Chiloplacus sp. expressed in ug dry weight.

Table 15. Growth data and logistic conversion factors for the growth curve for Chiloplacus sp. at 10°C. Each weight is the mean of 3 replicates each with a̲ 40 nematodes.

Age - days from hatching	Weight ug	% of estimated asymptote (0.5085 ug)	Logistic conversion factors
0	0.0084	1.59	-1.0216
4	0.0173	3.40	-0.8365
8	0.0418	8.22	-0.6032
12	0.0437	8.59	-0.5911
16	0.0811	15.95	-0.4154
20	0.1631	32.07	-0.1876
24	0.2407	47.34	-0.0266
28	0.3450	67.85	0.1867
32	0.4103	80.69	0.3577
36	0.4595	90.36	0.5597
40	0.5072	99.74	1.4916
44	0.5157	101.42	------
48	0.5001	98.35	1.0216
52	0.5016	98.64	1.0717
56	0.5001	98.35	1.0216
60	0.5260	103.44	------

T = 30.04 with 8 df

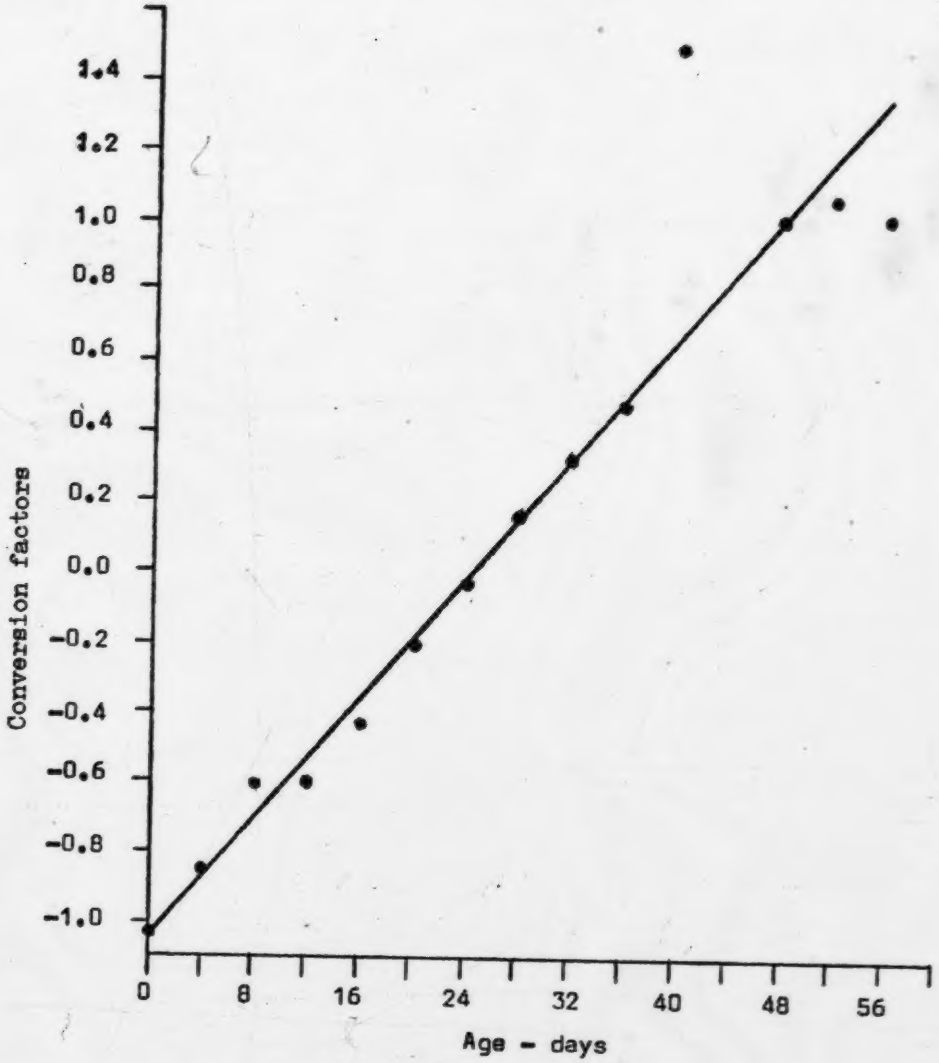


Fig. 6. The logistic conversion factors for the Chiloplacus sp. growth data at 10°C.

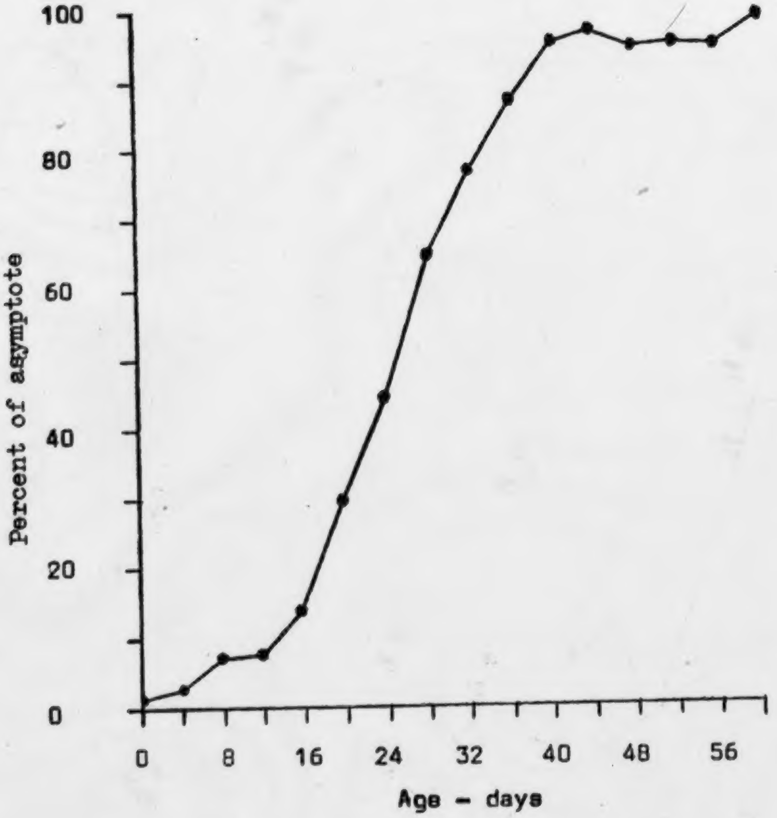


Fig. 7. Growth curve of Chiloplacus sp. at 10°C. expressed as percentage of the asymptote.

5.3.3 Reproduction of Chiloplacus sp. at 10°C

The mean duration (± standard deviation) of the egg stage was 16.8 ± 0.3 days, and the mean hatching success was 46.8 ± 7.8% (Fig. 8).

The observed and estimated total mean numbers (± standard deviation) of eggs laid per female were 38.3 ± 23.0 and 317.8 ± 89.2 respectively, and the observed and estimated total mean numbers of juveniles hatched were 130.8 ± 40.6 and 148.8 ± 41.6 respectively (Table 16).

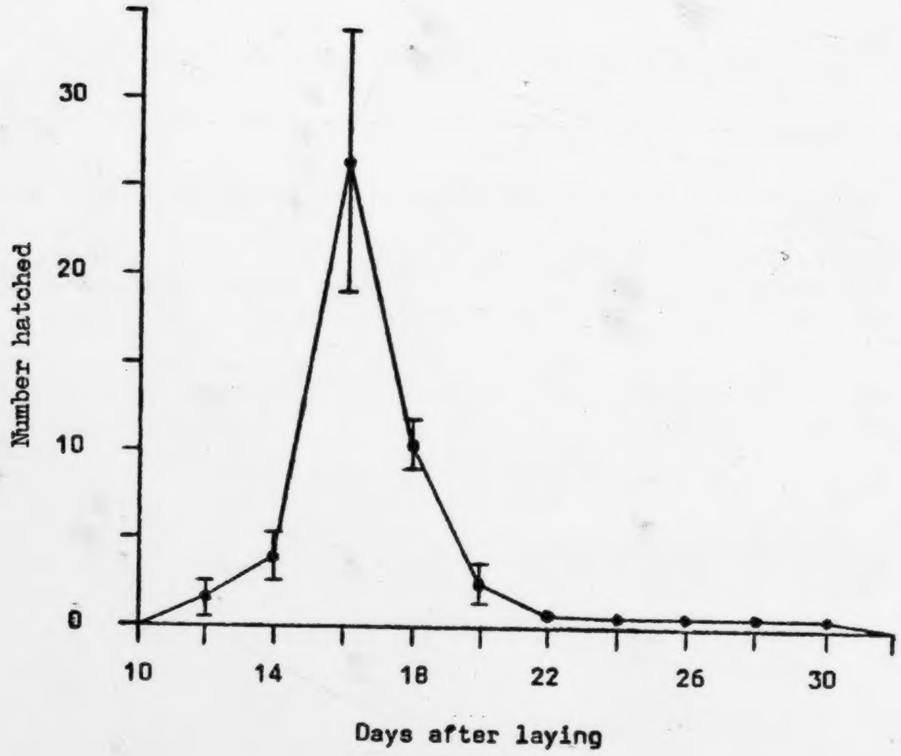
Net reproductive rate 'R_0' was 148.8 at 10°C (Table 17). The maximum age attained was approximately 99 days, beginning as new-laid eggs, and the reproductive period spanned approximately 56 days.

Intrinsic rate of increase 'r' was 0.09508 at 10°C, and mean length of generation 'T' was 52.6 days (Table 18).

The first three age groups, which spanned 12 of 56 reproductive days, contributed 80.58% of the value of r when r = 0.09508 (Table 19).

The stable age distribution of Chiloplacus sp. at 10°C when r = 0.0951 was 91.5% immatures and 8.5% adults (Table 20).

The instantaneous birth-rate 'b' was 3.92693, the instantaneous death-rate 'd' was 3.83185, and the finite rate of increase 'λ' was 1.09975.



Mean hatching time replicate^{-1} ± SD = 16.8 ± 0.3 days,
= 168 degree days
Mean hatching success replicate^{-1} ± SD = 46.8 ± 7.8%

Fig. 8. Duration of egg stage and hatching success for Chiloplacus sp. Each point is the mean of 5 replicates and includes the standard deviation. Temperature = 10°C.

Table 16. Mean number of eggs laid, and juveniles hatched by six Chilophacus sp. females during the reproductive period. The estimated numbers assume that 46.8% of the eggs laid do hatch.

	Number	± SD
Number of eggs observed and removed	38.3	23.0
Estimated no. of eggs that would have hatched (i.e. 46.8%)	18.0	10.6
Number of juveniles observed and removed	130.8	40.6
Estimated no. of eggs laid to produce observed no. of juveniles	279.5	87.0
Estimated no. of eggs laid	317.8	89.2
Estimated no. of juveniles hatched	148.8	41.6

Table 17. Life table age-specific fecundity rates of the egg-laying period, and net reproductive rate (R_o) for *Chiloplacus* sp. at 10°C.

Pivotal age in days (x)	(l_x)	(m_x)	($l_x m_x$)
43	0.468	26.00	12.1667
47	"	83.26	38.9680
51	"	42.32	19.8047
55	"	26.72	12.5067
59	"	29.65	13.8753
63	"	29.69	13.8967
67	"	27.48	12.8613
71	"	24.11	11.2833
75	"	8.49	3.9713
79	0.468	5.37	2.5140
83	0.390	6.27	2.4467
87	0.390	7.44	2.9007
91	0.390	2.76	1.0780
95	0.234	2.14	0.5000
99	0.078	——	——

R_o = 148.7734

Table 18. Calculation of intrinsic rate of increase 'r' for *Chiloplacus* sp. at 10°C by trial and error substitution in the expression $\sum e^{7-rx} l_x m_x = 1097$. Mean length of a generation, T, is calculated from $T = \frac{\log_e R_o}{r}$.

(x)	($l_x m_x$)	(7-rx)	(e^{7-rx})
43	12.1667	2.9116	18,3855
47	38.9680	2.5312	12.5691
51	19.8047	2.1509	8.5928
55	12.5067	1.7706	5.8744
59	13.8753	1.3903	4.0160
63	13.8967	1.0100	2.7455
67	12.8613	0.6296	1.8769
71	11.2833	0.2493	1.2832
75	3.9713	-0.1310	0.8772
79	2.5140	-0.5113	0.5997
83	2.4467	-0.8916	0.4100
87	2.9007	-1.2720	0.2803
91	1.0780	-1.6523	0.1916
95	0.5000	-2.0326	0,1310

r = 0.09508

T = 52.6 days

$$\sum_{43}^{95} e^{7-rx} l_x m_x = 1096.8$$

Table 19. The contribution of each age group to the value of r when r = 0.09508.

Pivotal age in days (x)	$(l_x m_x e^{7-rx})$	Percentage contribution of each age group
43	223.7	20.40
47	489.8	44.66
51	170.2	15.52
55	73.5	6.70
59	55.7	5.08
63	38.2	3.48
67	24.1	2.20
71	14.5	1.32
75	3.5	0.32
79	1.5	0.14
83	1.0	0.09
87	0.8	0.07
91	0.2	0.02
95	0.1	0.01
	1096.8	100.01

Table 20. Stable age distribution of Chiloplacus sp. at 10°C when $r = 0.09508$.

(x)	(l_x)	$(e^{-rm(x)})$	$(l_x e^{-rm(x)})$	Percentage distribution $100\beta l_x e^{-rm(x)}$
19	0.468	0.164225	0.0768573	31.662
23	0.468	0.112271	0.0525428	21.646
27	0.468	0.076753	0.0359204	14.798
31	0.468	0.052472	0.0245568	10.117
35	0.468	0.035872	0.0167880	6.916
39	0.468	0.024524	0.0114772	4.728
43	0.468	0.016765	0.0078460	3.232
47	0.468	0.011462	0.0053642	2.210
51	0.468	0.007836	0.0036672	1.511
55	0.468	0.005357	0.0025070	1.033
59	0.468	0.003662	0.0017138	0.706
63	0.468	0.002504	0.0011718	0.483
67	0.468	0.001712	0.0008012	0.330
71	0.468	0.001170	0.0005475	0.226
75	0.468	0.000800	0.0003744	0.154
79	0.468	0.000547	0.0002559	0.105
83	0.390	0.000374	0.0001458	0.060
87	0.390	0.000256	0.0000998	0.041
91	0.390	0.000175	0.0000682	0.028
95	0.234	0.000119	0.0000278	0.011
99	0.078	0.000082	0.0000063	0.003
			$1/\beta = 0.2427394$	100.000

/ 91.5% immatures /

8.5% total adults /

5.3.4 Population growth of *Chiloplacus* sp. at various temperatures

At 25°C the population increased from five to approximately 40,000 individuals in 42 days (Fig. 9). In contrast, at 0°C the initial five individuals did not reproduce during the six months of the experiment. At the intermediate temperatures, population growth rates were also intermediate.

The values of the intrinsic rate of increase, r, ranged from 0.0178 at 2°C, to 0.2131 at 25°C (Table 21). The value of r at 10°C was 0.0823.

The relation of r to temperature is described by the function:

$$r = 0.0088 + 0.0075T$$

The 95% confidence limits for 0.0088 are -0.0074 and 0.0250. According to this function population growth does not occur below -1.16 ± 1.80°C (Fig. 10). The regression coefficient is significant at $p = 0.01$, and its 95% confidence limits are 0.0043 and 0.0107, while the correlation coefficient = 0.9796.

Mean generation time at 10°C calculated from life table age - specific fecundity rates was 587.2 degree-days above -1.16°C (Table 22). Generation time at 10°C calculated from the population growth data was 678.3 degree-days. Observed cohort duration at 10°C was 1104.8 degree-days.

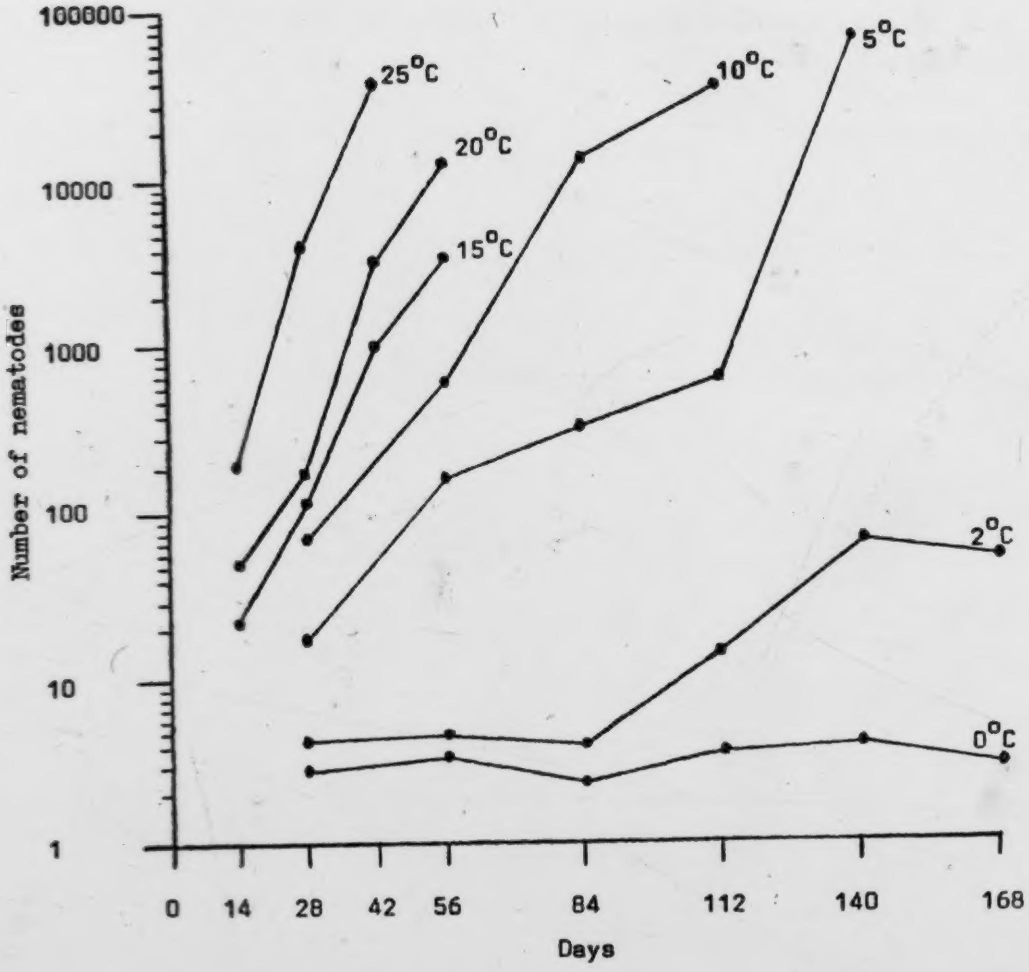


Fig. 9. Population growth of Chiloplacus sp. at various temperatures. Each experiment started at day zero with 5 adults, and each point is the mean of 3 replicates.

Table 21. Relation between population growth rate, r, and time at various temperatures for Chiloplacus sp., assuming that population growth is exponential.

	Temperature °C					
Parameter	2	5	10	15	20	25
r	0.0178	0.0605	0.0823	0.1216	0.1384	0.2131
a	2.0136	1.3078	1.8744	1.5214	1.7704	2.0136
Corr. coeff.	0.9824	0.9530	0.9905	0.9975	0.9922	0.9931

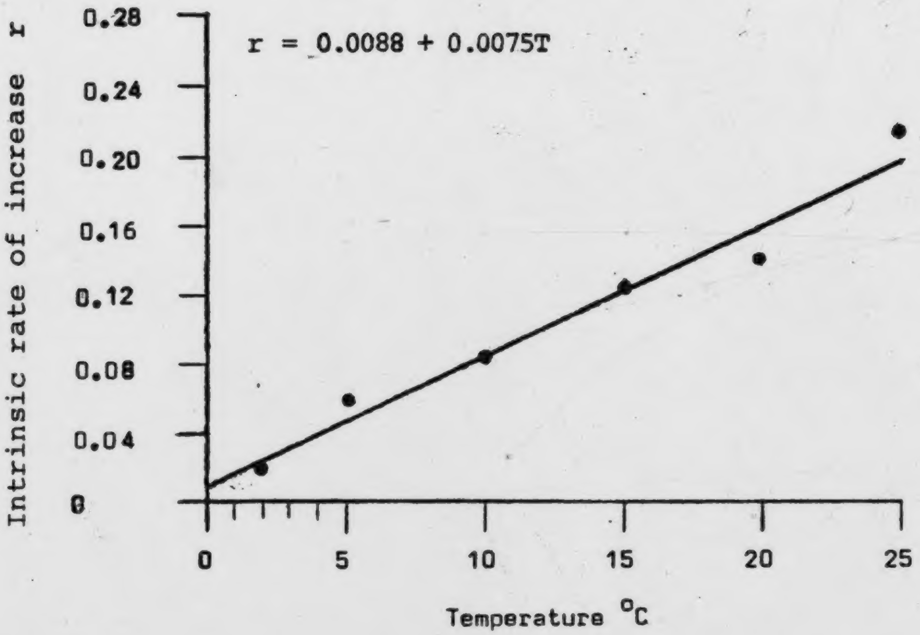


Fig. 10. Rate of population increase (r) as a function of temperature. When r = 0, T = -1.16353 i.e., there is no population growth at or below -1.16°C.

Table 22. Chiloplacus sp. generation time and cohort duration at 10°C expressed in degree-days above -1.16°C.

Mean generation time calculated from the life table age-specific fecundity rates.	587.2
Generation time calculated from the population growth data.	678.3
Observed cohort duration.	1104.8

5.4 Discussion

5.4.1 Form of the individual growth curve

Growth curves based on length have been drawn for several species of nematodes, including both parasitic and free-living forms (Bird, 1971; Fisher, 1970; Sohlenius, 1968, 1973a). These curves are typically sigmoid in shape, and the four steps of the hypothetical curve for nematode growth (Rogers, 1962; Lee, 1965), representing the four molts which normally occur before the adult stage is reached, are rarely apparent (Bird, 1971). Exceptions include species of *Cylindrocorpus* (Chin and Taylor, 1970) and *Acrobeloides nanus* (Sohlenius, 1973a), in which the four molts do occur as distinct steps. The linear growth curve I obtained for *Chiloplacus* sp. is of the smooth sigmoidal form.

Bird (1971) suggested that the common divergence from the hypothetical curve is because growth either is not interrupted by molting, as in *Caenorhabditis briggsae* (Jantunen, 1964), or does not occur between parasitic molts, as in *Meloidogyne* (Bird, 1959). According to Bird (1971), in most parasitic species greatest growth occurs after the last molt and molting tends to occur in the first half of the growth curve. Sohlenius (1968, 1973a) found that free-living species of rhabditida also continue to grow after the adult stage is reached. *Aphelenchus avenae* likewise grows substantially after the final molt (de Soyza, 1973), and I observed a similar pattern of development in Chiloplacus sp.

Few growth curves of free-living soil nematodes have been expressed in weight - I know of such information only for Aphelenchus avenae (de Soyza, 1973), and my own data for Chiloplacus sp. In both species the weight curves are sigmoid in form. Furthermore, the weight curve of Chiloplacus sp. is described by the logistic equation. Ricklefs (1968, 1973) showed that for birds a useful index of variation in the form of the growth curve is the location of the point of inflection in relation to the amount of growth accomplished. In many species of birds, as in Chiloplacus sp., the absolute rate of growth does not begin to decrease until half or more of the total growth has been attained. In other species the most rapid weight increase occurs early in the growth period and the point of inflection may be reached with less than one-third of total growth completed. The Gompertz growth equation (Laird, *et al.*, 1965) and, more particularly, the von Bertalanffy growth equation (von Bertalanffy, 1960; Fabens, 1965) are useful alternatives to the logistic equation, because they better fit growth curves exhibiting marked slowing of growth rate and prolongation of the growth period in the later stages of growth.

These equations are potentially powerful tools for making interspecific comparisons of growth (Ricklefs, 1967). For example, the pattern of the growth curve may be considered in terms of r selection and K selection, on the assumption that growth patterns are formed, at least in part by natural selection. Ricklefs' (1968) studies on birds demonstrate some of the possibilities of this kind of analysis. All 60 Passeriform species Ricklefs analyzed fell within the logistic group, as did most other small land birds and raptors. On the other hand, those species placed in the Gompertz and von Bertalanffy groups belonged predominately to the larger, more slowly growing Pelecaniformes, Ciconiiformes and Charadriiformes, but also included other species large for their orders.

Von Bertalanffy (1957) proposed three general weight growth types (which are dictated by three different metabolic types - see Chapter 6), encompassing more diverse animals. In von Bertalanffy's "first" metabolic/growth type, the weight curve is sigmoidal, with a point of inflection at about one third of the final weight. His "second" metabolic/growth type is characterized by exponential weight growth, and the "third" metabolic/growth type is, like his "first" type, characterized by sigmoidal weight curves. However, these latter sigmoidal curves lie between the "first" and "third" curves in form, that is, the points of inflection lie in the upper portions of the growth curves. The three growth equations used by Ricklefs (1967) I consider to be special cases of von Bertalanffy's "first" metabolic/growth types, insofar as their points of inflection lie at or below 50% of the final weight (von Bertalanffy's "first" metabolic/growth type receives a formal statement in the equation bearing his name - this equation I consider too restrictive to encompass the diversity of animals falling within his first metabolic/growth category, as Ricklefs with his studies of birds has shown).

At this point I wish to develop the idea that the weight growth curves used by Ricklefs represent an adaptive range of growth forms that is encompassed by a wider adaptive range represented by von Bertalanffy's growth types. For example, the exponential growth curve may be the ultimate strategy for the r selected organism. Using the logistic curve as a convenient starting point, progressive movement of reproduction forward in time will bring reproduction down to the point of inflection leading to, (1) the exponential curve, (2) reduced time to sexual maturity, and (3) reproductive maturity at a smaller size. On the other hand, the von Bertalanffy growth curve may represent the ultimate strategy for K selected organisms. Again starting with the logistic curve, movement of reproduction backward in time will (1) shift reproduction away from the point of inflection (which is at 30% of the asymptote on the von Bertalanffy curve), (2) increase time to sexual maturity, and (3) increase the size at which reproduction occurs. At the same time, freedom from the energy requirements of early reproduction may open the way for increased maximum size.

Exponential growth seems "good" strategy for very small organisms that are presumably subject to a greater number of adverse environmental factors than are large organisms. Swift growth through all stages presumably reduces the general vulnerability of small organisms. On the other hand, I find intuitively acceptable the idea that large organisms "need" exponential growth only in the very early part of the growth curve when they are relatively vulnerable.

This thesis needs qualification in the sense that no one group of organisms is likely to show the full range of curves described above. For example, birds appear to favour a fairly narrow range of sigmoid curves (Ricklefs, 1968). On the other hand, insects may favour the exponential end of the range. Evidently, the type of metabolism, among other factors, will concentrate a group of organisms in a reduced portion of the range of curves, as von Bertalanffy's (1957) thesis indicates. However, each group should show a range of curves, the factors governing which should operate on a broader scale between groups.

While acknowledging the lack of pertinent information on growth curves for nematodes, by analogy with birds I am prepared to predict how growth curve types may be distributed among free-living soil nematodes. Firstly, "extreme r strategists" such as the small, rapidly growing rhabditida (Johnson *et al.*, 1974) will have a preponderance of sigmoidal growth curves that tend towards the exponential curve (i.e. the points of inflection of the growth curves will generally lie between 50% and 100% of the asymptote). The rhabditid *Diplogaster nudicapitatus* is an example of this type of species (Sohlenius, 1968). Secondly, probable K strategists like the large, slow growing dorylaimids (Johnson *et al.*, *op. cit.*) and eudorylaimids will more frequently have growth curves best described by the Gompertz and von Bertalanffy equations (i.e. the points of inflection of the growth curves will generally lie between 0% and 50% of the asymptote). Finally, "intermediate" strategists like the tylenchids (Johnson *et al.*, *op. cit.*) should fall between the extreme r and K strategists in frequency of occurrence of the different growth types. In other words, logistic and very similar growth curves should be represented relatively frequently. Probable "intermediate" strategist

Chiloplacus sp. (*cf*. Sections 5.4.2, 5.4.3) has a growth curve best described by the logistic equation (this study).

Although the form of the growth curve is presumably an important indicator of a species' growth strategy, form alone is insufficient to adequately characterize the strategy. Growth rate and metabolic type need also to be considered in order to fully characterize growth. Furthermore, if an organism's growth is to be considered in the broader context of a general adaptive strategy, then fecundity and age-specific reproductive tactics must also be considered. I will consider these parameters further in these contexts in the remainder of this Chapter and in Chapter 6.

5.4.2 Growth Rate, Generation Time and Longevity

Species belonging to the Rhabditidae and Diplogasteridae are among the most rapidly growing of soil nematodes (e.g. Sohlenius, 1973b). *Rhabditis terricola* reared from newly laid eggs at 22°C, 15°C and 5°C, reached full size after 5, 8 and about 18 days respectively (Sohlenius, 1968). *Diplogaster nudicapitatus* grows even more quickly - it reached maximum size in about 3 days at 22°C (Sohlenius, *op. cit.*). Sohlenius found that *Rhabditis maupasi*, *Pelodera teres* and *Mesodiplogaster* sp. grew at about the same rate as *R. terricola*. Similarly, Chaung (1962) reported that *Rhabditis teres* completed development in about 3 days at 18°C. As might be expected, the generation times and longevity of these species are also short (e.g. Sohlenius, 1973b).

Tylenchids generally seem to develop more slowly than do the Rhabditidae and Diplogasteridae. Pillai and Taylor (1967) found that two species of *Ditylenchus* both required 25 days to reach sexual maturity at 20°C, and more than 90 days at 10°C. *Neotylenchus linfordi*, *Aphelenchus avenae* and *Paraphelenchus acontioides* needed 23,22 and 18 days respectively to attain maturity at 20°C, and all required more than 90 days at 10°C (Pillai and Taylor, *op. cit.*).

Species belonging to the Cephalobidae also develop more slowly than do the Rhabditidae and Diplogasteridae (e.g. Sohelnius, 1973b) and seem more comparable to tylenchids in their growth rates, generation times and longevity. *Acrobeles complexus* attained sexual maturity in 32 days at 25°C (Thomas, 1965). *Acrobeloides buetschlii* developed more quickly, taking 9-10 days at 25°C (Nicholas, 1962). *Acrobeloides nanus* took 11 days at 21°C and 21 days at 13°C (Sohlenius, 1973a), while *Cephalobus persegnis* required 12-13 days at 20°C (Popovici, 1972). For comparison, *Chiloplacus* sp. took 43 days to reach sexual maturity at 10°C, and completed growth in approximately 55 days.

Plectus parientinus (Plectidae) developed from egg to adult female in approximately 50 days at 10°-13°C, and required 60 days until eggs were again laid (Maggenti, 1961). Nielsen (1949) reported a development time of 20-25 days at 20-22°C for one species of *Plectus*, and approximately 20 days at 15-16°C for another species.

Less is known about the life histories of other groups. Johnson *et al.* (1974) noted that many dorylaimid species have relatively long life spans, citing unpublished information from their laboratory. *Mononchus aquaticus* (a dorylaimid), had generation times of 16, 20, 45 and 90+ days at 25°, 22°, 15° and 10°C respectively (Grootaert and Maertens, 1976). Several members of the Monhysteridae also have fairly long life spans. The marine species *Monhystera denticulata* had generation times of 10, 18 and 180 days (at optimum salinity) at 25°, 15° and 5°C (Tietjen and Lee, 1972). Similarly, *Monhystera disjuncta* had generation times of 13, 17 and 135 days at 17°-22°, 9°-12° and -1°-+1°C, while *Theristus pertenuis* took 23 and 47 days at the two higher temperatures (Tietjen and Lee, *op. cit.*). Neither species, incidentally, survived at 28°C. Finally, *Oncholaimus oxyuris* (Oncholaimidae) generation times varied between 101 days at 25°C and 570 days at 5°C (Heip *et al.*, 1978), and *Oncholaimus brachycercus* took 399 days at 7°C (Gerlach and Schrage, 1972).

On the basis of their rapid growth rates and short development times, many rhabditids justify classification as r strategists (i.e. Johnson *et al.*, 1974). By comparison, many tylenchids are better classified as "intermediate" strategists (Johnson *et al.*, *op. cit.*). To this intermediate category may be added several species of Cephalobidae, including *Chiloplacus* sp., and several species of *Plectus*. Only *Oncholaimus oxyuris* and *Oncholaimus brachycercus* of the species I mentioned above have exceptionally long development times. On this basis I consider these species obvious K strategists.

The above studies do not provide enough information to allow me to test my predicted relationships between the form of the growth curve and the rate of growth (cf. Section 5.4.1). However, several species hint at the possibilities. For example, the very rapidly growing rhabditid Diplogaster nudicapitatus had a length growth curve for which the point of inflection was very close to the asymptote (Sohlenius, 1968). In other words, most of the growth was exponential. The length growth curves of Rhabditis terricola showed less extreme forms of the same phenomenon. In contrast, growth of the more slowly developing Chiloplacus sp. was better represented by the logistic curve (Figure 7). Study of the form of the growth curves of species such as Oncholaimus oxyuris and the dorylaimids will throw further light on the problem.

Temperature clearly has a striking, and expected, effect upon nematode growth rates. For example, Monhystera denticulata showed an 18-fold increase in generation time when culture temperature was lowered from 25° to 5°C (Tietjen and Lee, 1972). However, the above data also illustrate more subtle developmental responses to lowered temperature. Sohlenius (1968) noted that the upper and lower limits for reproduction and development differ between species. For example, Thomas (1965) found that the lower temperature threshold for Acrobeles complexus was between 10° and 15°C, thereby agreeing with Wallace's (1961) general conclusion that the minimum temperature of phytoparasitic nematodes is about 10-15°C. *Tylenchus emarginatus* did not reproduce below 10°C (Gowen, 1970), and *Diplogaster nudicapitatus* did not lay eggs at 5°C (Sohlenius, 1968). Other species have even lower thresholds. *Chiloplacus* sp. grow and reproduced at 2°C but not at 0°C (this study). The marine nematode *Monhystera disjuncta* grew and reproduced at -1°-+1°C (Gerlach and Schrage, 1971).

Of particular note is the observation that species with relatively lowered upper and lower temperature thresholds may develop more rapidly than do species with higher thresholds when they are reared at the same temperatures. For example, *Chiloplacus* sp. had a generation time of 52.6 days at 10°C (Table 18), and *Monhystera disjuncta* took 17 days at 9°-12°C (Gerlach and Schrage, 1971). By comparison, two species of *Ditylenchus*, *Aphelenchus avenae*, *Neotylenchus linfordi* and *Paraphelenchus acontioides* all had generation times greater than 90 days at 10°C (Pillai and Taylor, 1967).

Some cold-adapted poikilotherms (particularly aquatic organisms) metabolize much faster than would be predicted by extrapolating the metabolic rates of warm-adapted species down to low temperatures (e.g. Hochachka and Somero, 1973). Evidently, rate compensation to temperature may occur in growth as well as in respiration (*cf*. Hochachka and Somero, *op*. *cit*.).

Nematodes from Arctic and Alpine terrestrial ecosystems probably have lower than average temperature thresholds for growth, reproduction and activity. These nematodes should likewise have relatively high growth rate compensation to temperature. Nematodes from cold freshwater and marine habitats may be similarly characterized. On the other hand, in nematodes of hot deserts and tropical rain forests, both upper and lower thresholds should be relatively high. However, nematodes of hot deserts may also have a relatively large range between thresholds, with some growth rate compensation at low temperatures, because of the wide diurnal range of temperatures they encounter.

Temperature is not only an important determinant of growth rate, but it also affects the amount of growth in several species of nematodes. Some nematodes grow substantially larger at lower temperatures than they do at higher temperatures. For example, at 35°C *Panagrellus silusiae* males averaged 1.60 mm in length, and females 1.90 mm (Gysels, 1964). However, *P. silusiae* attained greatest length at 10°C, with males reaching 1.94 mm, and females 2.53 mm. The effect of temperature upon size of *Rhabditis terricola* is even greater (Sohlenius, 1968). At 25°, 22°, 15° and 5°C, the average female lengths were 1.13 mm, 1.27 mm, 1.78 mm and 2.08 mm respectively. Similarly, females of *Cephalobus nanus* averaged about 0.45 mm in length at 22°-23°C, and approximately 0.55 mm at 15°-17°C (Popovici, 1973). Chiloplacus sp. also grew larger at lower temperatures, although I did not attempt to quantify my observations.

Hochachka and Somero (1973), in explaining seasonal low temperature metabolic compensation, offer a physiological basis for increased growth at low temperatures. They observed that because basal or maintenance metabolism is reduced at low temperatures, poikilothermic organisms probably need not maintain as high a metabolic rate at low temperatures as they do at higher temperatures. If maintenance metabolism is reduced at low temperatures, the organism may be able to channel a larger share of its food into the synthesis of energy storage compounds, such as fats, and into protein synthesis (i.e. "growth"). Selection in cold environments presumably favours organisms which are able to redirect their metabolic flow in ways consistent with maximal use of their ingested food (cf. Hochachka and Somero, op. cit.). Nematodes characteristic of cold environments (e.g. species of the genus Plectus) may have greater capacity for adaptation of this kind than do nematodes characteristic of warm environments.

If the phenomenon of increased size in response to reduced temperatures is widespread among nematodes, it offers one explanation for the high individual biomass of arctic nematodes (cf. Chapter 4.4.1). On the basis of this argument, alpine nematodes can also be expected to have relatively high individual biomass. Conversely, nematodes of hot deserts and tropical rain forests should have relatively low individual biomass compared with nematodes of other ecosystems. This trend, incidently, offers the possibility of a nematode/invertebrate analogue of Bergmann's rule (cf. Villee et al., 1978).

5.4.3 Fecundity and Reproductive Effort

Nematodes vary widely in their fecundities (e.g. Paramonov, 1962). Among the tylenchids there are species of *Anguina* which produce up to 2,500 eggs per female (Paramonov, *op. cit.*). Many species of rhabditids and heteroderids may be equally fecund. Other species are more moderately fecund, including *Chiloplacus* sp. which produces an average of 318 eggs per female (this study), *Cephalobus persegnis* with 299 eggs per female (Popovici, 1972), and *Aphelenchus avenae* which averages 199+ eggs per female (Fisher, 1968). Most tylenchids also have moderate fecundities (Paramonov, *op. cit.*). Species with low fecundities include *Acrobeloides nanus*, with approximately 40 eggs per female (Sohlenius, 1973a), and *Oncholaimus oxyuris* with approximately 30 eggs per female (Heip *et al.*, 1978). Gerlach and Schrage (1971) studied 6 free-living marine nematodes whose fecundities ranged from 16 to 36 eggs per female.

The limited data available suggest a correlation between nematode size, longevity and fecundity. Among bacterial feeding nematodes at least, most species of Rhabditidae and Diplogasteridae both grow faster and have higher fecundities than do the Cephalobidae (e.g. Sohlenius, 1973b). Dorylaimids tend to be large and many have few offspring in addition to relatively long life spans

(Johnson *et al*., 1974). The large *Oncholaimus oxyuris* also has low fecundity in addition to being relatively long-lived (Heip *et al*., 1978). While more data are needed to establish the generality of these trends, the above information supports Johnson *et al*. (*op*. *cit*.) in their classification of rhabditids as extreme r strategists, and tylenchids as a group as intermediate strategists (*cf*. Section 5.4.1).

The evolution of reproductive tactics has received considerable attention during the last decade (e.g. Gadgil and Solbrig, 1972; Pianka and Parker, 1975; Hirshfield and Tinkle, 1975). Reproductive effort, as a key component of an organism's reproductive tactics, has drawn much of this attention. Nematode reproductive effort is difficult to assess from published information, because the weights of adult females and their eggs are rarely given. I made a crude estimate of reproductive effort for *Chiloplacus* sp. using the ratio of adult tissue to reproductive tissue produced (*cf*. Tinkle and Hadley, 1975). The ratio for this species was 1:5.75. The same ratio for *Aphelenchus avenae*, calculated from de Soyza's (1973) production data, was 1:2.13. Acknowledging the lack of pertinent information, I am prepared to suggest trends in the ratio among other nematodes. While the weight of the mature egg relative to the weight of the adult may be inversely related to fecundity (e.g. fewer but larger, "fitter" offspring - Pianka, 1978), I expect nematode reproductive effort be roughly proportioal to fecundity. In other words, rhabditids and heteroderids will have very high ratios, tylenchids generally moderate ratios (e.g. similar to the ratios of *Chiloplacus* sp. and *A. avenae*), and dorylaimids will usually have low ratios.

Temperature not only affects the size attained by some nematodes (cf. Section 5.4.2), but also affects the amount of energy some species expend in reproduction. Several species lay fewer eggs at lower temperatures. *Oncholaimus oxyuris* at 25°, 20°, 15°, 10° and 5°C averaged 36.8, 34.3, 18.5 and 13.5 eggs per female respectively (Heip *et al*., 1978). Similarly, *Panagrolaimus rigidus* at 20°C laid 111 eggs, and at 10°C laid 8 eggs (Mianowska, 1976). *Monhystera denticulata* laid 18-24 eggs at 15°C, and 10-17 at 5°C (Tietjen and Lee, 1972). At 22° and 15°C *Rhabditis terricola* produced 258 and 150 eggs respectively (Sohlenius, 1966). *Acrobeloides nanus* (Sohlenius, 1973a) and *Cephalobus nanus* (Popovici, 1973) also laid fewer eggs at lower temperatures.

Rhabditis terricola, *Acrobeloides nanus* and *Cephalobus nanus* are particularly interesting because they show both increasing size and declining reproductive effort with falling temperature. Assuming that these animals have a finite amount of energy that can be flexibly apportioned to different processes (cf. Section 5.4.2), when the amount of energy assigned to one process is changed, then the amount assigned to other processes may also be changed. There seems little doubt that different metabolic pathways within the same organism have very different responses to temperature (i.e. have different Q_{10} values) (Hochachka and Somero, 1973). Reproductive rate may be more temperature sensitive than growth rate (and will therefore have a higher Q_{10}). Reproduction probably also has a higher low temperature threshold than does growth (e.g. Pattee et al., 1973). As temperature declines, the more rapid suppression of reproductive effort will make more energy available for growth. This "freed" energy may augment the increased growth accruing from lowered metabolic maintenance requirements at low temperatures (cf. Section 5.4.2). The two mechanisms combined therefore constitute a more powerful, albeit tentative, explanation of my proposed nematode/invertebrate analogue of Bergmann's rule. As such, this explanation is very different from the one given for Bergmann's rule (e.g. Villee et al., 1978).

Nematodes evidently offer interesting opportunities for studying the apportioning of energy between growth and reproduction. Some nematodes may also be particularly suitable for the experimental study of the "cost" of reproductive effort in terms of mortality of the reproducing females (cf. Pianka and Parker, 1975). For example, sexually isolated adult females of Rhabditis terricola (which reproduces sexually) lived for about 12 days at 20° and 15°C, but the longest time an egg-laying female lived was 7 days (Sohlenius, 1968). In this species maximum reproductive output seems to require the continuous presence of males, which makes possible the experimental manipulation of reproductive effort.

5.4.4 Age-specific Reproductive Tactics

Several species of nematodes other than *Chiloplacus* sp. have been shown to begin egg-laying substantially before reaching maximum size. *Aphelenchus avenae* reared at 26°C began egg-laying at the age of 6 days, but ceased growing at 10 days (de Soyza, 1973). In other words, this species began egg-laying at 51.53% of final weight. *Rhabditis terricola* reared at 15°C began egg-laying at 5-6 days, but completed growth at approximately 9 days (Sohlenius, 1968). Similarly, *Acrobeloides nanus* reared at 13°C reached adulthood in 12 days (i.e. accomplished the 4th molt), began egg-laying at 15-16 days, and attained maximum length at approximately 21 days (Sohlenius, 1973a). It is not clear from the literature that early reproduction is universal among nematodes, but I expect it is a common occurrence.

The shifting of the start of reproduction to progressively earlier parts of the growth curve seems an obvious evolutionary strategy for r selected organisms, because shortening generation time is an effective way of increasing the intrinsic rate of increase, r (e.g. Southwood, 1976). Furthermore, the closer the onset of sexual maturity approaches the point of inflection of the growth curve, the more closely it becomes associated with the most rapidly attained portion of growth. In other words, loss of size at onset of maturity is compensated for by the maximum possible growth rate to maturity. Holometabolous insects, whose larvae appear highly specialized for efficient growth, and which probably have exponential growth curves (e.g. von Bertalanffy, 1957), may represent the culmination of my suggested evolutionary trend, albeit at a higher level of organization. This kind of specialization, incidently, may help account for Fenchel's (1974) observation that animals at higher levels of organization have higher values of r than do animals of the same size at lower levels of organization (_cf_. Chapter 9.2). For contrast with my proposed extreme r strategy, modern western man offers an example of extreme K strategy. Because of changing economic and social mores, reproduction is being progressively shifted far past both the onset of reproductivity maturity and the attainment of maximum size.

In predicting the size/age at onset of reproduction relative to the size/age at cessation of growth among free-living soil nematodes, I suggest the following patterns (_cf_. Section 5.4.1): (1) extreme r strategists like the rhabditida will begin reproduction at either (a) relatively small size or, (b) relatively close to the point of inflection of the growth curve; (2) K strategists like the dorylaimids will begin reproduction at either (a) relatively large size or, (b) relatively distant from the point of inflection of the growth curve; and (3) intermediate strategists like the tylenchids, *Chiloplacus* sp., and *Aphelenchus avenae*, will fall between the r and K strategists in these characteristics.

Chiloplacus sp. accomplished 47.68% of egg production before growth ceased (i.e. about 12 days), and completed the remainder in the following 44 days (Table 18). For comparison, *Aphelenchus avenae* (at 26°C) accomplished 33.37% of egg production before growth ceased (i.e. 5 days), and produced the remaining eggs over 15 days (de Soyza, 1973).

The value of "early" reproduction is demonstrated by Table 19. In *Chiloplacus* sp. the first 4 days of reproductive life account for 20.40% of the value of r, the first 8 days account for 65.16%, and the first 12 days account for 80.58%. By contrast, the last 4 day interval contributes 0.01%. The significance of the data in Table 19 is that the intrinsic rate of increase is determined to a much greater extent by the rate of egg-laying in the first 12 days of adult life than by the total number of eggs laid, even though only 47.68% of egg production was accomplished in the first 12 days (*cf*. Birch, 1948). Eggs laid in successive time intervals make reduced contributions to r. In the case of *Chiloplacus* sp., for each egg laid in the first 4 days of adult life, it requires 1.46 times as many eggs in the second interval to make the same contribution to the value of r, $(1.46)^2$ in the third interval, and $(1.46)^{n-1}$ in the nth interval (*cf*. Birch, *op*. *cit*.). The ratio 1.46:1 is the ratio between successive weighting values e^{7-rx} per egg in Table 18 (Birch, op. cit.).

Birch (1948) presented comparable data for the rice weevil Calandra oryzae which emphasizes the importance of the early rate of egg-laying in determining the value of r. In this species only 27% of the eggs were laid in the first 2 weeks, but these eggs contributed 85% of the value of r. The ratio between successive weighting factors was 2.1:1.

The above analysis permits quantitative assessment of the effects on the intrinsic rate of increase of changes in the time of reproduction, rate of reproduction, fecundity, and the form of the survivorship curve. In other words, this analysis is a means of distinguishing between different components of r and K strategies.

Compared with Chiloplacus sp., I expect r strategist nematodes to have higher rates of egg-laying in the early part of the reproductive period. The reproductive period may also be relatively short. Many of the very fertile rhabditids, anguins and heteroderids are also distinguished by highly synchronized egg production (Paramonov, 1962). On the other hand, K strategist nematodes probably have lower early rates of egg-laying and more extended egg-laying, than do intermediate strategists like Chiloplacus sp. My predictions lead, on the one hand, to the conventional r strategy of a single short reproduction and, on the other, to the conventional K strategy of repeated reproduction (e.g. Pianka, 1978).

An important ability in r selected nematodes living in very cold environments may be the capacity to maintain high early rates of egg-laying at low temperatures. For example, *Acrobeloides nanus* had a high early rate of egg-laying at 21°C, but a much reduced early rate at 13°C, even allowing for the fact that fewer eggs were produced at 13°C (i.e. 57% of the 21°C output) (Sohlenius, 1973a). Similarly, *Panagrolaimus rigidus* had a high early egg-laying rate at 30°C, a somewhat reduced early rate at 20°C, and a uniform rate throughout the reproductive period at 10°C (Mianowska, 1976). This means that for these species the intrinsic rate of increase at the lower temperatures will be lower than at the higher temperatures by an amount greater than expected from the decline in temperature alone. By comparison, the pattern of egg-laying of *Chiloplacus* sp. at 10°C resembled that of *A. nanus* at 21°C, and that of *P. rigidus* at 30°C.

5.4.5 The Intrinsic Rate of Natural Increase, r

The length of the developmental stages, the reproductive effort, the age schedule of fecundity and the life table of a species, may all be embodied in the single function, the intrinsic rate of natural increase, r. Different values of r incorporate different patterns of these parameters and represent different adaptive and evolutionary strategies. These different strategies were first given coherent expression as r selection and K selection by MacArthur and Wilson (1967).

There are very few published estimates of r for nematodes and, apart for my data for *Chiloplacus* sp., I know of no such information for free-living soil nematodes. Heip *et al*. (1978) estimated r for *Oncholaimus oxyuris* at 25°, 20°, 15°, 10° and 5°C, and obtained corresponding values of 0.0286, 0.0220. 0.0154. 0.0086 and 0.0026 per day. Natural populations of *Chromadorina germanica* had r values ranging from 0.098 to 0.167 over the 20°-30°C temperature range, while for *Chromodora macrolaimoides* the r value at 25°C (and 26 $^{\circ}/_{\circ\circ}$ salinity) was 0.15 (Tietjen and Lee, 1977).

Noteworthy is the wide range of r values exhibited by *Oncholaimus oxyuris*, and by *Chiloplacus* sp. (Table 21). In *O. oxyuris* a rise in temperature of 20°C caused an 11-fold increase in the value of r. For *Chiloplacus* sp. a 23°C rise in temperature resulted in a 14-fold increase in r. These data illustrate the striking impact that temperature has on the value of r, and emphasizes that r must be expressed in terms of a particular temperature. Moreover, r should be expressed in terms of a particular environment. Andrewartha and Birch (1954) demonstrated that different humidities, as well as different temperatures, affected the value of r in two grain beetles *Calandra oryzae* and *Rhizopertha dominica*. Apart from temperature, environmental factors likely to be of special importance in determining the r values of soil-living nematodes are moisture and food supply.

Clearly it is possible to determine an array of values of r for different combinations of physical and biotic factors. However, of particular significance will be the value of r obtained when fecundity and survival are greatest, because this will be the species' maximum rate of increase, r_{max} (Birch, 1948). The conditions under which r_{max} is attained will presumably be those conditions to which the organism is best adapted. For many organisms r_{max} is probably a theoretical potential only, but in some environments, including temperate and arctic habitats, some organisms may periodically be able to attain r_{max} (Birch, *op. cit.*).

Apart from the adaptive significance of r_{max}, the r values of a species offer a means of quantifying that species' relative fitness in other environments. Patten (1975) hypothesized that linearization of ecosystems is evolutionarily adaptive, in the sense that natural selection acts against nonlinear characteristics. Insofar that intrinsic rates of increase are linear functions of temperature (Heip, 1977) and, presumably, of other environmental factors, departure and magnitude of departure from a linear relationship indicates relative fitness. The slope of the linear relationship will also indicate relative fitness - the shallower the slope, the greater being the relative fitness.

On the basis of the above explanation, I make the following predictions for nematodes: (1) species adapted to cold climates will attain r_{max} at lower temperatures than will species of warm climates; (2) species adapted to variable climates (e.g. temperature) will have broader linear relationships between r and the environmental variable, than will species of constant environments; and, (3) in species adapted to constant environments, the linear component of the r-environmental variable relationship may be flatter than in species adapted to variable environments. In this context I noted that the magnitude of the difference between the r values of Oncholaimus oxyuris and Chiloplacus sp. remained constant from 25° to 15°C, but from 15° to 5°C the r values of O. oxyuris declined progressively more rapidly relative to Chiloplacus sp. The r values of Chiloplacus sp. bore a linear relationship to temperature from 25° to 2°C (Figure 10).

The r values of Chiloplacus sp. were, on average, 10.5 times larger than those of Oncholaimus oxyuris at the same temperatures. Even this limited information shows that nematodes may vary greatly in their r values. However, very few estimates of r have been made for nematodes. To complete my thesis I will summerize the material and ideas I have presented by predicting trends in r values for some of the major groups of nematodes. Firstly, species belonging to the Rhabditidae and Diplogasteridae, and some of the very fecund tylenchids, will have very high r values, perhaps several orders of magnitude greater than those I obtained for Chiloplacus sp. Secondly, many tylenchids, plectids, and species of Cephalobidae will have intermediate r values, placing them near Chiloplacus sp. Some species of Monhysteridae will undoubtedly also have moderate r values. Thirdly, many dorylaimids probably have moderate to low r values. Low r values, incidentally, may enable communities to support high densities of large predatory species (e.g. Heip et al., 1978). This may explain how several arctic communities are able to support large populations of dorylaimids and eudorylaimids (cf. Chapter 2.3.1). Finally, several species of the Oncholaimidae undoubtedly have very small r values, which are at least an order of magnitude smaller than those of Chiloplacus sp.

It is informative to consider the r/body weight ratios of *Oncholaimus oxyuris* and *Chiloplacus* sp. in the wider context of the general evolution of r. Fenchel (1974) studied the relationship between r and body weight in a wide range of organisms, and obtained separate linear equations for unicellular organisms, poikilothermic metazoa, and homoiothermic metazoa. These equations are distinguished primarily by progressively higher values for r from unicellular organisms to homoiothermic metazoa. The equation for poikilothermic metazoa is $\log r = -1.6391 - 0.2738 \log W$, in which r is per day, and W is the wet weight in gm. Using this equation Heip *et al*. (1978) determined that the theoretical value of r for an animal of the size of an adult of *O. oxyuris* is 40 times higher than the mean annual value they measured, and 15 times higher than the maximum value at the highest temperature. Heip *et al*. suggested that the large deviation indicates a real difference between the reproductive rate of *O. oxyuris* and similarly sized poikilotherms. Similarly, the largest value of r I obtained for *Chiloplacus* sp. was only one quarter of the theoretical value. My results therefore support the possibility that nematodes have lower intrinsic rates of increase than do poikilothermic metazoa as a whole.

On the basis of the analyses I have presented in this Chapter, I feel justified in treating *Chiloplacus* sp. as an intermediate species in terms of r and K selection. Consequently, Chiloplacus sp. is a valid "average" nematode for the purposes of estimating nematode population energy flow in Arctic terrestrial communities.

Chapter 6

RESPIRATION RATES OF *CHILOPLACUS* SP. AND OTHER ARCTIC NEMATODES

6.1 Introduction

As in the case of growth, reproduction and population growth (Chapter 5), respiration rates of Arctic free-living soil nematodes have not been studied at the temperatures the nematodes normally encounter. In this chapter I present low-temperature respiration information for *Chiloplacus* sp., and similar information for representative samples of the nematode fauna as a whole. The primary purpose of the studies on *Chiloplacus* sp. was to produce the respiration information required by the Ryan and Whitfield production model (Ryan, 1977a) to estimate nematode production. The required information included (1) a function relating respiration to changing weight, and (2) a function relating respiration to changing temperature.

Earlier attempts to estimate nematode production in cold environments were based on respiration rates estimated from data obtained at relatively high, non-arctic temperatures, using extrapolation techniques such as Krogh's standard metabolic curve (*cf*. Lagerlöf *et al*., 1975; Procter, 1977a). The information I present in this chapter avoids some of the limitations of these indirect estimates of low-temperature respiration rates.

While I treated the respiration data of Chiloplacus sp. as representative of High Arctic free-living soil nematodes for the purpose of estimating production, I also measured respiration rates of samples of the fauna as a whole, in order to assess the validity of using Chiloplacus sp. as a representative nematode.

In addition to measuring respiration of Chiloplacus sp. at low temperatures, I obtained respiration data for this species at high temperatures to permit direct comparison with similar information for temperate and tropical nematodes. These studies were designed to help determine whether nematodes living at high latitudes show adaptation of metabolic rate relative to similar species living at lower latitudes (cf. Scholander et al., 1953; Procter, 1977b). In addition, the combined high- and low-temperature respiration information provide a partial test of the validity of Krogh's (1941) standard metabolic curve as a low-temperature extrapolation technique.

6.2 Methods

I measured oxygen consumption using the volumetric microrespirometer described by Gregg and Lints (1967). I conducted the studies of Chiloplacus sp. at 2°, 5°, 10°, 15°, 20° and 25°C, and those on the representative samples of the nematode fauna at 5°, 10° and 15°C. A Haake Unitherm thermoregulator with cooling coil maintained the experimental temperatures within ± 0.25°C. Respiration chambers of ≙ 100 ul volume, reduced to ≙ 50 ul volume by addition of space fillers, accommodated the experimental animals. The apparatus was sensitive to change in gas volume of 0.0015% h^{-1}. Because individual nematode oxygen consumption was usually less than this rate, I studied several specimens together to obtain measurable rates.

For the studies of Chiloplacus sp. the experimental animals were drawn from cultures maintained at the appropriate temperatures in Freas Low Temperature Incubators (i.e. Chapter 5.2). The nematodes for the general faunal studies were also acclimated in these incubators, but were maintained in the soil samples obtained from Truelove Lowland. This material, which was previously frozen for storage, was thawed and placed in the appropriate incubators a minimum of one week before the experiments.

All animals were collected immediately before experimentation and were allowed to equilibrate with the system for one hour before readings were taken. Three respirometers were operating simultaneously, with one left empty to serve as control for thermal and barometric changes. A minimum of three readings at 30 or 60 min intervals were taken respirometer^{-1} temperature^{-1}.

Dry weights were obtained with a Cahn G2 Electrobalance accurate to 0.05 ug, after drying for 24 hr at 80°C with calcium chloride.

The function relating respiration of *Chiloplacus* sp. to weight at 10°C was based on 22 replicates spanning the range of weights encompassed by newly hatched (24 h old) second stage larvae and mature adults. The relationship was quantified by means of a regression curve fitted according to procedures given by Sokal and Rohlf (1969).

The function relating respiration rate of *Chiloplacus* sp. to temperature was based on three or four replicates at each of the five temperatures studied, while the comparable function for the representative nematode samples was based on four replicates at each of the three temperatures investigated. I used the respiration rate/weight function obtained for *Chiloplacus* sp. at 10°C to standardize weight prior to fitting regression curves to the respiration rate/temperature data (Sokal and Rohlf, *op. cit.*).

I compared the respiration rates of *Chiloplacus* sp. at 2°, 5°, 15°, 20° and 25°C by means of a single classification anova with unequal sample sizes, following procedures given by Sokal and Rohlf (1969). Following the anova, I used the Student-Newman-Keuls Test to make multiple comparisons among the means (Sokal and Rohlf, op. cit.). Finally, I compared the oxygen consumption of a 1 ug individual at 10°C, which I obtained from the respiration rate/weight regression curve, with the 5° and 15°C respiration data using a test described by Sokal and Rohlf for comparing a single observation with the mean of a sample.

I used Van't Hoff's Q_{10} approximation to calculate the effect of changing temperature on respiration rate (Grodzinski et al., 1975).

The respiration information I used in the Ryan and Whitfield model (Ryan, 1977b) to estimate production was based on (1) the mean dry weight at which Chiloplacus sp. begins egg-laying (Chapter 5), and (2) the mean seasonal dry weight of the nematode fauna (Chapter 4.3). These weights were 0.2928 ug and 0.4297 ug respectively.

6.3 Results

6.3.1 Respiration of Chiloplacus sp. as a function of weight at 10°C

The relationship between respiration (R) and weight (W) is represented by the equation:

$$\log R = -3.0693 + 0.8844 \log W$$

where R is in ul O_2 ind^{-1} hr^{-1}, W is in ug ind^{-1}, -3.0693 (log oxygen consumption of an individual of 1 ug dry wt) is the intercept, and 0.8844 is the slope of the log-log plot of respiration versus weight (Fig. 11). The 95% confidence limits for -3.0693 are -3.2752 and -2.8634. The regression coefficient is significant at $p = 0.01$, its 95% confidence limits are 0.6764 and 1.0924, and the coefficient of determination is 0.7892.

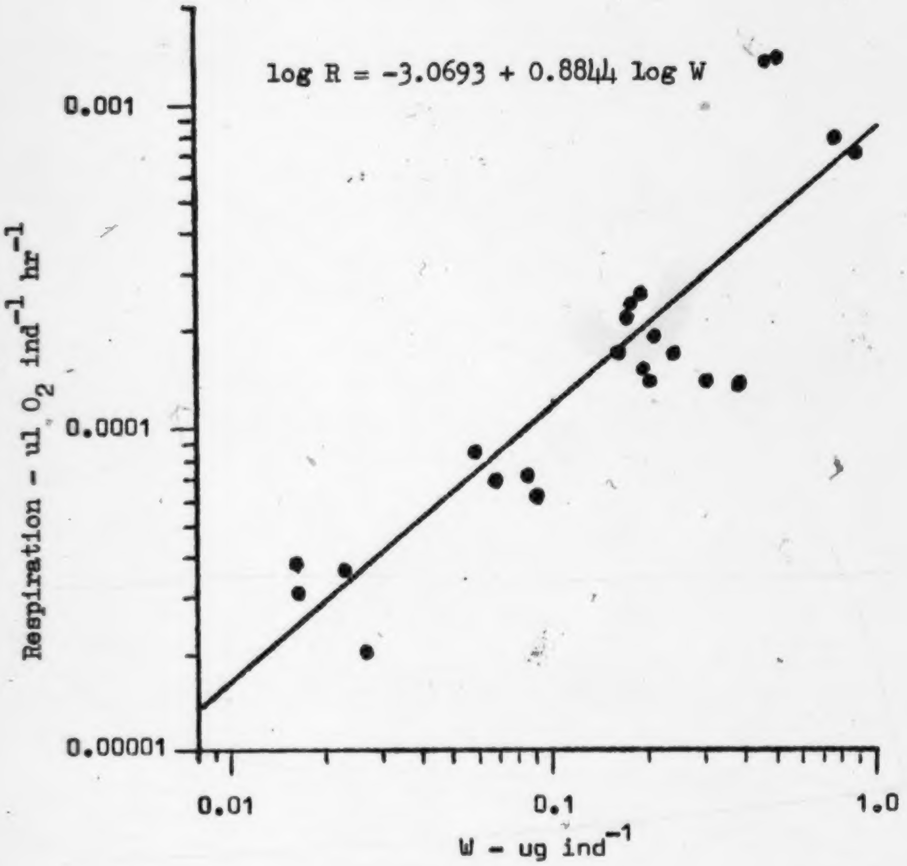


Fig. 11. Respiration of Chiloplacus sp. as a function of dry weight at 10°C.

6.3.2 Respiration of Chiloplacus sp. as a function of temperature

Oxygen consumption ranged from 0.2470 x 10^{-3} µl ind^{-1} hr^{-1} at 2°C, to 2.2845 x 10^{-3} µl ind^{-1} hr^{-1} at 25°C, for a nematode weighing 1.0 µg (Fig. 12). I concluded from the anova that there is a significant (p = 0.01) added variance component among temperatures for Chiloplacus sp. respiration rates. According to the Student-Newman-Keuls Test all the differences between the means are significant at p = 0.05, except for the 2°-5°C, and 20°-25°C differences. The 10°C and 5°C mean respiration rates are significantly different at p = 0.01, but the difference between the 10°C and 15°C rates are not significant at p = 0.05.

The relationship between respiration (R) and temperature (T) is represented by the equation:

$$\log R = -3.6661 + 0.0453T,$$

where R is in O_2 ul ind^{-1} hr^{-1}, T is in °C, -3.6661 (log oxygen consumption of an individual of 1 µg dry wt at 0°C) is the intercept, and 0.0453 is the slope of the plot of log respiration versus weight (Fig. 12). The 95% confidence limits of -3.6661 are -3.7263 and -3.6059. The regression coefficient is significant at p = 0.01, and the 95% confidence limits are 0.0336 and 0.0564. The coefficient of determination is 0.9903.

Q_{10} values ranged from 0.95 for the 10°-15°C temperature interval, to 6.29 for the 5°-10°C interval, while the value for the 2°-25°C interval was 2.89 (Table 23).

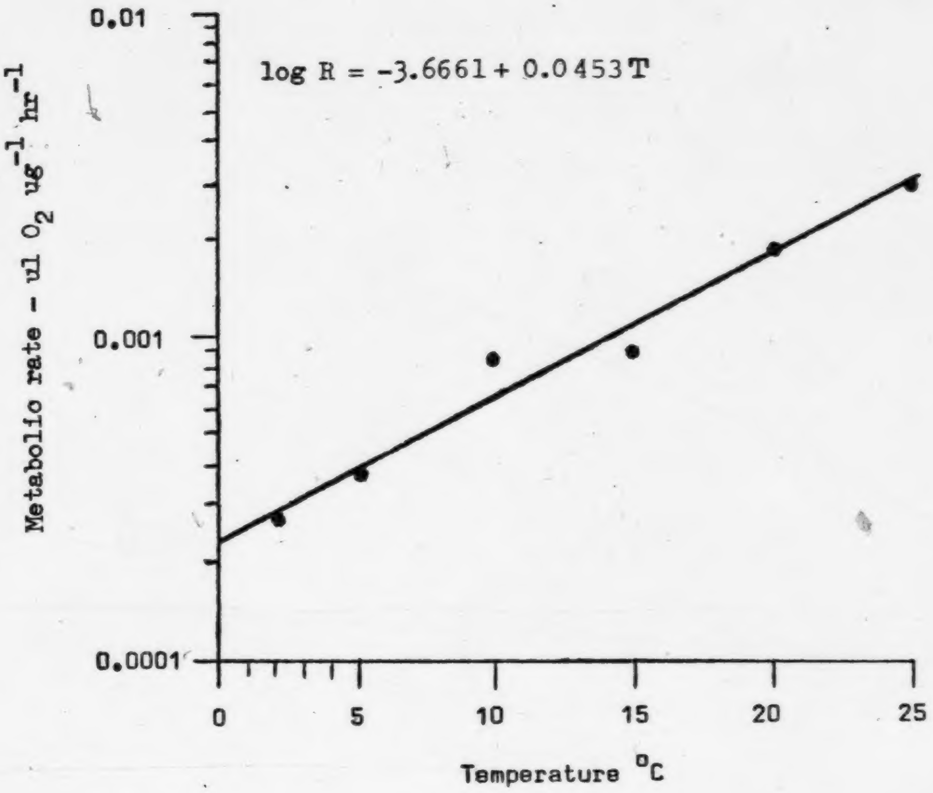


Fig. 12. Metabolic rate as a function of temperature for Chiloplacus sp. The respiration rates are for a 1.0 ug animal, and have been converted using the function log R = -3.0693 + 0.8844 log W. Each point is the mean of 3-4 replicates.

Table 23. Q_{10} values for Chiloplacus sp. at six temperature intervals.

2-5°C	5-10°C	10-15°C	15-20°C	20-25°C	2-25°C
2.90	6.29	0.95	4.90	2.40	2.89

6.3.3. Respiration of representative samples of the nematode fauna as a function of temperature

Average oxygen consumption was 0.1593×10^{-3} ul ind^{-1} hr^{-1} at 5°C, 0.3603×10^{-3} ul at 10°C and 0.5332×10^{-3} ul at 15°C for a nematode of 0.4297 ug dry wt (Fig. 13). The relationship between respiration (R) and temperature (T) is represented by the equation:

$$R = -0.00002297 + 0.00003739T,$$

where R is in ul O_2 ind^{-1} hr^{-1}, T is in °C, -0.00002297 (oxygen consumption of an individual of 0.4297 ug dry wt at 0°C) is the intercept, and 0.00003739 is the slope of the plot of respiration versus weight. The 95% confidence limits of -0.00002297 are -0.00003761 and -0.00000833. The regression coefficient is significant at $p = 0.02$, and its 95% confidence limits are 0.00002265 and 0.00005203. The coefficient of determination is 0.9970.

The Q_{10} values were 5.12 and 2.19 for the 5°-10°C and 10°-15°C intervals respectively, while the value for the 5°-15°C interval was 3.35 (Table 24).

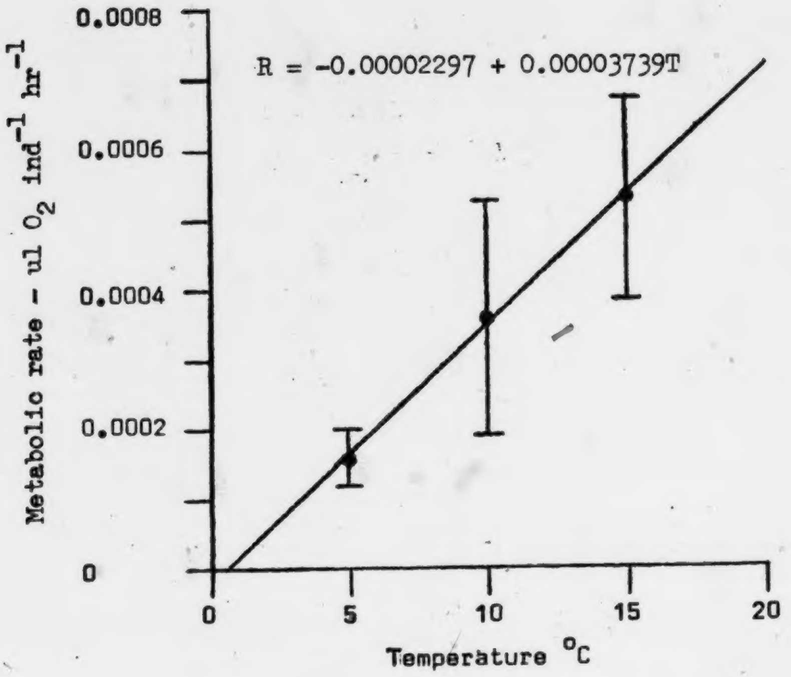


Fig. 13. Metabolic rate as a function of temperature for mixed nematode species from the field. The rates are for an animal of 0.4297 ug dry weight, and have been converted using the function log R = -3.0693 + 0.8844 log W. Each point is the mean of 4 replicates.

Table 24. Q_{10} values for mixed nematode species from the field at three temperature intervals.

5-10°c	10-15°C	5-15°C
5.12	2.19	3.35

6.4 Discussion

6.4.1 Respiration and Weight

The oxygen consumption per unit body weight (i.e. metabolic rate) of many organisms changes as body size changes (e.g. Zeuthen, 1953; von Bertalanffy, 1957; Hemmingsen, 1960). Generally, metabolic rate declines in non-linear relationship to weight as weight increases, as appears the case for many species of nematodes. Values for the exponent of weight dependency, b, for nematodes when respiration is regressed on weight include the following: Panagrolaimus rigidus, b = 0.64 (Klekowski et al., 1974); Tobrilus gracilis, b = 0.69 (Schiemer and Duncan, 1974); Enoplus communis, b = 0.68 (Wieser and Kanwisher, 1960); Aphelenchus avenae, b = 0.85 (de Soyza, 1970 - In: Schiemer and Duncan, 1974); and various species of benthic marine nematodes, b = 0.987 (Ott and Schiemer, 1973). For Chiloplacus sp. the value of the weight exponent b = 0.88 (Figure 11). These data demonstrate the diversity of values for the weight exponent exhibited by nematodes.

Some organisms show non-linear relationships between metabolic rate and size. The pea aphid Acyrthosiphon pisum exhibits rapidly increasing metabolic rate during early growth, and then declining metabolic rate subsequently (Randolph et al., 1975). Some nematodes may also have "atypical" patterns of metabolic rate. Zeuthen (1955) interpreted data for *Pontonema vulgare* as showing a value of $b = 0.4$ in larvae, and $b = 1.0$ in mature adults. Wieser and Kanwisher (1960) reported a similar change in the exponent with increasing body size for *Enoplus communis*. Both interpretations have been criticized because neither was tested by statistical analyses, and intermediate values for the full size ranges were not disproved (Hemmingsen, 1960; Atkinson, 1976).

Chiloplacus sp. provides tentative support for a non-linear relationship between respiration rate and weight (Figure 11). While my data are accounted for statistically by the single exponent $b \doteq 0.88$, a quadratic function may better fit the data, thereby establishing the non-linearity of the relationship (no quadratic function gave a significantly better fit - Jorgensen, pers. comm.). When the mature adults are excluded from the analysis, $b = 0.73$ for the juveniles and very young adults. Increasing egg production probably raises the value of a in mature, rapidly reproducing adults. At the peak of egg production up to 25% of the weight of the female of *Chiloplacus* sp. may be comprised of developing eggs. Any relatively fecund species of nematode with highly synchronized egg production is likely to have a markedly increased value during part of adulthood (e.g. particularly some tylenchids and heteroderids - *cf*. Chapter 5.3.3). Consequently, the average value of the exponent is also likely to be relatively high in these species.

Hemmingsen (1960) noted that the relationship between respiration and weight sometimes departs significantly from his "typical" poikilotherm exponent b = 0.75 over limited size ranges.

The reasons why metabolic rates frequently decline with development are uncertain. Referring to Acyrthosiphon pisum, Randolph et al. (1975) suggested that "... perhaps either greater proportions of low-metabolic rate tissues or lower proportions of high-metabolic rate tissues are produced in the last half of pre-reproductive and reproductive life". While the pattern of metabolic rate in A. pisum is probably a special case, I have little doubt that the proportion of low metabolic rate structural supporting tissue increases in most organisms as they develop (cf. Chapter 9.3). Reduction in the effectiveness of surface-dependent processes as the animal grows larger may also contribute to declining metabolic rates. This may be particularly pertinent for nematodes, which lack specialized respiratory and circulatory organs. For example, the length of the diffusion pathway in the animal increases as it grows.

The relationship between metabolic rate and increasing size when different species are compared is also controversial (e.g. Zeuthen, 1947; Hemmingsen, 1960). Zeuthen (op. cit.) recognized three groups of poikilotherms: acellular forms with surface-proportional metabolism (b = 0.67); some small metazoa with weight-proportional metabolism ($b = 1.0$); and larger poikilotherms with surface-proportional metabolism ($b = 0.67$), but with higher metabolic rates than acellular animals. Hemmingsen (1960), however, applied a common interspecific exponent of $b = 0.75$ to poikilotherms above 0.1 gm dry weight. Hemmingsen suggested that this component is an evolutionary compromise between the advantages of maintaining a high level of metabolism with increasing size, and the limitations imposed by the reduced effectiveness of surface dependent processes. Increasing proportions of low-metabolic rate supporting tissues with increasing species size, as in the case of growing animals, will also contribute to decreasing metabolic rate (*cf*. Chapter 9.3).

The value of the weight exponent in interspecific nematode comparisons is also controversial (e.g. Atkinson, 1976). Both Zeuthen (1953) and Hemmingsen (1960) placed nematodes in the small group of poikilotherms with weight-proportional metabolism. Some recent workers have rejected a weight-proportional metabolism in nematodes (e.g. Klekowski *et al*., 1972; Atkinson, 1976). Klekowski *et al*. (*op*. *cit*.) obtained an interspecific exponent of $b = 0.72$ for a variety of free-living and plant parasitic nematodes. Atkinson (*op*. *cit*.) re-analyzed the data of several authors and obtained a value of $b = 0.79$. This value is significantly different from $b = 1.0$ and $b = 0.67$, but does not differ from $b = 0.75$

which is commonly used to relate body size and metabolism in poikilotherms (i.e. Hemmingsen, 1960). By contrast, Ott and Schiemer (1973) obtained interspecific values of $b = 0.805-1.028$ for several groups of benthic marine nematodes, thereby providing recent evidence of weight proportional metabolism in nematodes. I suggest that because these nematodes are probably anaerobes (e.g. Schiemer and Duncan, 1974), they are thereby largely freed from the constraints of surface-limited processes. Of course, any nematode with anaerobic capabilities will tend towards weight-proportional metabolism. However, despite their apparent metabolic diversity, nematodes as a group probably lie between weight-proportional and surface-proportional metabolism.

Nematodes not only differ in their values for the weight exponent when their respiration-body weight regressions are compared, but they also differ in their values for the regression coefficient, a, which gives the level of oxygen consumption. For example, the values of "a" for *Aphelenchus avenae* (de Soyza, 1970 - In: Schiemer and Duncan, 1974), *Panagrolaimus rigidus* (Klekowski *et al*., 1974), *Enoplus communis* (Wieser and Kanwisher, 1960) and *Tobrilus gracilis* (Schiemer and Duncan, 1974) at 20°C were 1.343, 2.020, 1.566, and 0.522 respectively. Ott and Schiemer (1973) obtained a value of $a = 0.636$ for a general regression for 24 species of benthic marine nematodes at 20°C, and Klekowski *et al*. (1972)

obtained a general value of a = 1.40 for 68 species of free living nematodes at the same temperature.

Several groups of nematodes are distinguished by unusually high or low rates of oxygen consumption. Klekowski *et al*. (1972) observed that predaceous species are located above the general regression line, and suggested that this is because of their greater mobility. Some benthic aquatic nematodes undoubtedly have relatively low respiration rates (e.g. Ott and Schiemer, 1973; Schiemer and Duncan, 1974). Schiemer and Duncan (*op*. *cit*.) suggested that the freshwater species *Tobrilus gracilis* is a partially obligate anaerobe, even in the presence of oxygen, as an adaptation to life in habitats of low oxygen or anoxic conditions.

The value of a = 1.40 obtained by Klekowski *et al*. (1972) for 68 species of free living nematodes makes interesting comparison with equivalent information for other invertebrates. For unicellular organisms of the same weight at the same temperature (i.e. 20°C), Hemmingsen (1960) gave a standard value of a = 0.52. Similarly, for metazoan poikilotherms in general, he estimated a standard metabolism of a = 4.17. Evidently nematodes have a level of metabolism which is substantially higher than that of unicellular organisms, but which is substantially lower than that of poikilothermic metazoa in general (*cf*. Atkinson, 1976). The increased size of nematodes compared with unicellular organisms has presumably been accompanied both by increased tissue specialization for improved functional efficiency, and by increased maintenance costs. Their metabolic rates are presumably associated with these trends (e.g. Fenchel, 1974). The same reasoning also explains the still higher metabolic rates of larger poikilotherms, such as the insects, compared with nematodes.

The relatively low metabolic rates of nematodes, compared with most poikilothermic metazoa, complements the observation that nematodes have lower intrinsic rates of natural increase than do most poikilotherms of the same size (e.g. Heip *et al*., 1978; and this study - *cf*. Chapter 5.4.4). These findings are pertinent in terms of efficiency of energy utilization by heterotrophs in some Arctic communities, because nematodes are the dominant metazoa in some trophic levels in these communities. I develop this theme in Chapter 9.

6.4.2 Respiration and Growth

Von Bertalanffy (1957) related the metabolic types represented by the exponents b = 0.67, b = 1.0 and b between 0.67 and 1.0, to three growth types. In each case the metabolic type dictates the course of growth as expressed in the form of the linear and weight growth curves.

In von Bertalanffy's first metabolic type, respiration is proportional to weight, according to the surface law (i.e. b = 0.67). When the animal is small, surface-proportional anabolism prevails over weight-proportional catabolism, and the animal grows. As the animal grows, the ratio between surface and weight shifts against surface, and the energy remaining for growth decreases. Eventually a steady state is reached where anabolism and catabolism balance each other, and growth ceases. Solution of the growth equation gives a linear growth curve that is a decaying exponential without a turning point. The weight growth curve is sigmoid, with a point of inflection at about one third of the final weight (cf. Chapter 5.4.1).

In the second metabolic type, respiration is proportional to weight (i.e. b = 1.0). Consequently, anabolism and catabolism, both being weight-proportional, run at the same pace. Therefore both linear and weight growth are exponential, and no steady state is reached (in those insect larvae which show exponential growth, metamorphosis may terminate growth).

Finally, in the third metabolic type, respiration is intermediate between surface and weight proportionality (i.e. $0.67 < b < 1.0$), and solution of the growth equation produces sigmoidal linear and weight growth curves.

Because Chiloplacus sp. had an intermediate value for the exponent (regardless of whether one accepts $b = 0.88$, or $b = 0.73$ as representative), it fits von Bertalanffy's "third" metabolic type. Furthermore, because Chiloplacus sp. had both linear and weight growth curves of sigmoidal form (*cf*. Chapter 5.4.1), this species supports the relationship between respiration and growth that von Bertalanffy expressed in his third metabolic/growth type.

I noted in Chapter 5.4.1 that the larvae of holometabolous insects probably tend towards exponential weight growth curves as one specialization for rapid and efficient growth. According to von Bertalanffy's second metabolic/growth type, these organisms are likely to have weight proportional metabolism as the causal factor. The larvae of some holometabolous insects have little elaboration of supporting tissues with increasing size (e.g. higher Diptera), and are also inactive compared with the adults. Consequently, they may be able to sustain weight-proportional metabolism throughout growth.

The immature stages of hemimetabolous and ametabolous insects presumably compromise efficient growth through progressive development of adult structures, and the additioal requirements of greater activity. Consequently, these groups should show less frequent and less comprehensive weight-proportional metabolism and exponential growth (e.g. *Acyrthosiphon pisum* has exponential growth and respiration only in the early larval stages - Randolph *et al.*, 1975). In other words, hemimetabolous and ametabolous insects are most likely to fit von Bertalanffy's "third" metabolic growth type, as does *Chiloplacus* sp.

I noted in Chapter 5.4.1 that some small very fast growing nematodes, such as some tylenchids, may have sigmoidal weight growth curves which tend towards the exponential curve in form (e.g. *Diplogaster nudicapitatus* - Sohlenius, 1968). According to Bertalanffy's thesis, these nematodes should therefore have relatively high values for the exponent b. The structural and physiological advantages of being relatively small (*cf.* previous section) may be relevant here. Small nematodes may have a higher proportion of high-metabolic rate tissues than do larger nematodes (e.g. *Oncholaimus oxyuris* - Heip *et al.*, 1978), because they require relatively less supporting tissue. Similarly, small nematodes may benefit from a more favourable surface-volume ratio. However, immature nematodes, whether small or large, are committed to an essentially adult form and function, as are the nymphs of hemimetabolous and ametabolus insects. Consequently, even small nematodes cannot attain the level of commitment to efficient growth that has been reached by some holometabolous insect larvae. On the basis of these arguments, I predict that the weight exponent of extreme r selected nematodes will approach b = 1.0, whereas in extreme K selected species it will approach b = 0.67. It is worth reiterating here that the large and highly synchronized reproductive effort of r selected nematodes will help raise the value of b.

The limited data on nematode exponent/body size associations offer partial support for my expectations. For example, the "intermediate" strategists Chiloplacus sp. (this study) and Aphelenchus avenae (de Soyza, 1970) had "intermediate" values for the exponent of b = 0.88 and b = 0.85. The weight ranges of these two species were 0.0084-0.5085 ug dry weight, and 0.02-1.33 ug wet weight respectively. For the larger nematodes Panagrolaimus rigidus (Klekowski et al., 1974), Tobrilus gracilis (Schiemer and Duncan, 1974), and Enoplus communis (Wieser and Kanwisher, 1960), b = 0.67, 0.69 and 0.68 respectively, while their weight ranges were 0.02-2.01, 0.07-3.19 and 1.33-91.59 ug wet weight, respectively.

In making my predictions I accept neither Hemmingsen's "universal" value of b = 0.75 for poikilotherms of more than 0.1 gm dry weight, nor Atkinson's tacit acceptance of this value for nematodes. Similarly, while the general regression equation of Klekowski *et al*. (1972), in which b = 0.72, may be suitable as a first approximation in estimating the maintenance requirements of nematode communities, I do not consider it suitable for comparative studies of species. I believe that the metabolic diversity of nematodes, and of invertebrates in general, is too great to be so narrowly defined, and I consider that the great range of b-values in the literature illustrate this apparently unrecognized diversity.

6.4.3 Respiration and Temperature

The respiration-temperature curve of *Chiloplacus* sp., despite being adequately characterized by a linear regression (Figure 12), resembles the more complex curves frequently observed in poikilothermic organisms (for citations see Wieser, 1973). These curves characteristically rise steeply in the lower temperature range, flatten in the middle range, and then rise again in the higher temperature range (Wieser, *op. cit.*). The common occurrence of higher Q_{10} values in the lower temperature range have been emphasized by Scholander *et al.* (1953), and others (see also Chapter 8.3). Usually the Q_{10} is well above 2, and often between 6 and 10, in the lower range, but only between 1 and 2 in the middle range (Wieser, *op. cit.*). The distribution of Q_{10} values for *Chiloplacus* sp. undoubtedly fits this pattern (Table 23), although I must acknowledge that I require more data points to be completely satisfied with this interpretation.

Wieser (1973) has provided a comprehensive analysis of this form of respiration-temperature curve. According to Wieser, this curve closely resembles the respiration curve of mitochondria as they change from "state 3" to "state 4" (see Pye, 1973). Pye characterized state 3 by large amounts of ADP *in vivo* which would result from high rates of ATP hydrolysis in energy-requiring processes. On the other hand, in state 4 ATP accumulates and the energy charge is high. In this state, if no further ATP-requiring reactions are mobilized, energy consumption, and therefore the Q_{10}, will attain a steady state that is essentially independent of temperature (Wieser, op. cit.). High Q_{10} values therefore represent the ability to adjust energy consumption with great sensitivity to temperature changes. Warming rapidly accelerates ATP-consuming processes and cooling results in equally rapid deceleration.

Wieser suggests that it is significant that high Q_{10} values are so frequently encountered at the low end of the biological temperature range (see Chapter 8.3), where poikilotherms must increase their metabolism as rapidly as possible following cold torpor, but must arrest it equally quickly if temperature falls. (In this context it is worth noting that smaller poikilotherms, like nematodes, may be able to respond sooner to rises in environmental temperature than can larger poikilotherms, because their smaller size and greater surface-to-volume ratio facilitates faster warming. Smaller size will also increase the range of favourable microclimates - possibly an important consideration in relatively spartan Arctic environments.) Compensation in terms of "positive control" may require too much energy in this phase. However, Wieser allows that true compensatory control of metabolism at low temperatures may occur, particularly in animals that spend their lives at low temperatures (e.g. Scholander et al., 1953). Chiloplacus sp., with its unusually low Q_{10} between 2° and 5°C, hints at such low-temperature "positive control".

Wieser considers that the plateaus in the respiration-temperature curves of poikilotherms represent adaptive mechanisms for saving energy. If the curves were to continue with the same temperature coefficient in this phase as is typical of the cold phase, the organism would expend a disproportionate amount of energy during occasional peak temperatures. He notes that such plateaus are best developed in animals which must economize their energy reserves, such as animals of tidal habitats, which can renew their energy stores only periodically.

Since nematodes of Arctic terrestrial habitats, and particularly of wet terrestrial habitats, are often necessarily perennial, they too may be considered to have intermittent access to energy supplies. Extending the analogy, they may also need relatively well-developed plateaus, as Chiloplacus sp. apparently does, in order to save energy.

The temperature-insensitive regions of the curve are likely to occur at the temperatures most commonly encountered by the animal. Chiloplacus sp. appears least temperature-sensitive at 10°-15°C. Soil temperatures on the raised beach are for much of the summer season quite steady in this range (e.g. Courtin and Labine, 1977). By comparison, species characteristic of the meadow probably have plateaus at lower temperatures, while species from temperate and tropical habitats presumably have plateaus at higher temperatures.

There is little published information on nematode respiration rates with which to compare my data for *Chiloplacus* sp. The respiration of *Chiloplacus* sp. at 20°C was lower than the average rate determined by Klekowski *et al*. (1972), but it was not significantly lower. Bhatt and Rohde (1970) measured respiration rates for four species of plant parasitic nematodes. Three of these species had respiration rates near that of *Chiloplacus* sp. at 10°C (i.e. 0.0005-0.0015 ul O_2 ug^{-1} hr^{-1} - compared with 0.00085 ul for *Chiloplacus* sp.), while the fourth species, *Ditylenchus dipsaci*, was much higher with 0.0032 ul. However, the first three species had indetectable respiration rates at 5°C, although *D. dipsaci* remained high with 0.0026 ul. On the other hand, the plant parasites, except for *Anguina tritici*, had much higher respiration rates at higher temperatures. For example, at 22°C these species had metabolic rates ranging from 0.0053 to 0.0074 ul at 22°C, compared with 0.0023 ul for *Chiloplacus* sp. at the same temperature.

This information for nematodes, although limited, supports the common observation that poikilothermic organisms from cold environments show metabolic rate compensation to temperature (e.g. Hochachka and Somero, 1973). Chiloplacus sp. undoubtedly maintains higher respiration rates at low temperatures than do some plant parasitic nematodes from warmer environments (the exception, D. dipsaci, lives in more temperate conditions than do the other species - Bhatt and Rohde, 1970). However, Chiloplacus sp. falls far short of complete metabolic rate compensation to temperature because its maximum metabolic rate at its average environmental temperature does not approach the rates attained by the other species at their higher average environmental temperatures. As a corollary to this difference, the low Q_{10} values of Chiloplacus sp. above 10°C, compared with the other species, may reflect its superior homeostatic capabilities developed in response to a greater need for protection from excessive energy utilization at high temperatures.

I expected Chiloplacus sp. to have relatively high respiration rates between 0° and 10°C because this physiological capability is an obvious complement to this species' ability to grow and reproduce in this temperature range (cf. Chapter 5.4). On the other hand, the low respiration rates of plant parasitic nematodes below 10°C likewise complements their general inability to grow and reproduce at these temperatures (cf. Chapter 5.4).

My respiration information for the samples of the nematode fauna as a whole essentially supports my conclusions (Figure 13, Table 24). These samples had metabolic rates at 5-15°C that were similar to those I obtained for Chiloplacus sp., although the collective metabolic rate probably declines more rapidly below 5°C. On the basis of these results I feel justified in treating Chiloplacus sp. as "representative" for the purposes of estimating energy flow through Arctic nematode populations. These results complement my finding that Chiloplacus sp. is "intermediate" in terms of r and K strategies (Chapter 5.4.4).

Chapter 7

FIELD ESTIMATES OF NEMATODE RESPIRATION AND PRODUCTION

7.1 Introduction

In this chapter I present estimates of average annual respiration and production for the nematode faunas of the raised beach and meadow. Continuing the theme that these study areas represent different, widespread, tundra communities, I also predict nematode respiration and production expected in the communities. I used information for other invertebrates obtained from the same habitats (Ryan, 1977a), to determine relative contribution of nematodes to invertebrate respiration and production in these communities. Similarly, I used Ryan's information to predict total invertebrate production in these communities. Finally, I compared nematode production in tundra communities with production in temperate and tropical communities.

The nematode respiration and production estimates presented in this chapter, and the data on which they are based, supersede previously published information (Procter, 1977a). In making both the present and earlier estimates, I used the Ryan and Whitfield production model (Ryan, 1977a, 1977c). A secondary purpose of this chapter is to assess the validity of some of the assumptions of the Ryan and Whitfield model, particularly as they apply to nematodes, but also in terms of invertebrates in general. For example, the model assumes that the rate of weight gain of an individual organism is exponential. In Chapter 5 I showed that for *Chiloplacus* sp., and *Aphelenchus avenae* (de Soyza, 1973), rate of weight gain is logistic in form.

7.2 Methods

The Ryan and Whitfield production model (Ryan, 1977a, 1977c), has the general form:

$$R = cP$$

where R = respiration,

P = production,

c = constant relating respiration to production.

The 'synthetic cohort' (Ryan, 1977a) is the basic unit of the model, for which juvenile and adult contributions to respiration and production are estimated separately. Juvenile respiration is given by:

$$R = \frac{a\, N_o W_o^{\,b}}{(b\beta - \alpha)} \left[\left(\frac{W_f}{W_o} \right)^b \frac{N_f}{N_o} - 1 \right]$$

where N_o = number of individuals (newly hatched larvae) entering the cohort,

N_f = number of individuals reaching maturity,

W_o = mean dry weight in micrograms of the individuals entering the cohort,

W_f = mean dry weight in micrograms of the individuals reaching maturity,

b = rate at which specific metabolic rate per unit weight changes relative to weight as weight increases,

β = growth rate,

α = death rate,

and a = constant relating respiration to weight, which is calculated from:

$$R = aW^b$$

where R = microlitres of oxygen per individual per hour at 10°C,

and W = mean individual dry weight in micrograms.

Juvenile production is obtained from:

$$P = \frac{N_o W_o^{\alpha/\beta}}{(1-\alpha/\beta)} \left[W_f^{1-\alpha/\beta} - W_o^{1-\alpha/\beta} \right]$$

with the symbols defined as in the respiration equation.

The constant c is given by:

$$c = \frac{F.\ R/P.\ 1000}{4.7}$$

where F = calories per milligram ash-free dry weight of nematode tissue,

R/P = ratio of respiration to production,

1000 = converts milligrams to micrograms, and millilitres to microlitres,

and 4.7 = number of calories per millilitre of oxygen (Petrusewicz and Macfadyen, 1970).

Initially I used the following data obtained from my studies of Chiloplacus sp. to estimate the juvenile contribution to cohort respiration and production (in lieu of my own data, I used literature information as noted):

N_o = 1488,

N_f = 10,

W_o = 0.0084 ug,

W_f = 0.2928 ug

b = 0.8844,

R = 0.3000×10^{-3} ul ind^{-1} hr^{-1},

W = 0.2928 ug ind^{-1},

a = 0.8889,

F = 3.679 cal mg^{-1},

R/P = 1.17 (recalculated from Marchant and Nicholas, 1974; and de Soyza, 1970),

c = 915.84.

Adult respiration is obtained from:

$$R = \frac{\bar{N}\ a\ \bar{W}^b\ T\ 0.0047}{1000}$$

where $\bar{N}$ = mean number of adults,

$\bar{W}$ = mean dry weight in micrograms of the adults,

and T = duration of the adult stage in hours above 0°C.

The other symbols and values remain as previously defined.

Adult production which, in terms of the Ryan and Whitfield model, constitutes only the eggs which failed to hatch, is calculated from:

N_e = number of eggs which failed to hatch,
and W_e = mean individual dry weight in micrograms of newly laid eggs.

For my initial estimates of adult respiration I used the following data:

N_o = 10,
N_f = 0.5,
$\bar{W}$ = 0.4623 ug,
T = 1120 hrs;

and I used the following data in estimating adult production:

N_e = 1680,
W_e = 0.0092 ug.

For the other parameters I used the juvenile values.

Because the mean individual dry weight of the cohort as defined above (i.e. 0.0269 ug) was less than the mean weight I obtained for the field population (i.e. 0.4297 ug), for my final cohort respiration and production estimates I increased the pertinent input data by the appropriate correction factor. This involved multiplying the above egg, juvenile, and adult weights by 15.9187:

W_e = 0.1465,
W_o = 0.1337,
W_f = 4.6610,
$\bar{W}$ = 7.3592.

The other data were unchanged.

I expressed cohort production efficiency in terms of the productivity coefficient (i.e the ratio of gross productivity to total respiration - Larcher, 1975).

For cohort duration I used the cohort time I observed for Chiloplacus sp. (i.e. 1104.8 degree-days). I tested the model's performance by comparing the model's estimate of the duration of the juvenile stage with my observed duration for this stage (i.e. 479.9 degree-days).

I calculated annual respiration and production per m^2 for the study areas according to Ryan (1977a). These calculations, which incorporated the density estimates presented in Chapter 3, and the temperature data of Courtin and Labine (1977), I performed as follows:

$$\text{cohorts m}^{-2} = \frac{\text{nematodes m}^{-2}}{\bar{N}\text{ cohort}^{-1}}$$

where $\bar{N}$ = mean number of nematodes per cohort;

$$\text{cohorts m}^{-2}\text{ season}^{-1} = \frac{\text{degree-days season}^{-1}}{\text{degree-days cohort}^{-1} \times \text{cohorts m}^{-2}};$$

$$\text{respiration m}^{-2}\text{ season}^{-1} = \text{cohorts m}^{-2} \times \text{respiration cohort}^{-1};$$

and

$$\text{production m}^{-2}\text{ season}^{-1} = \text{cohorts m}^{-2} \times \text{production cohort}^{-1}.$$

7.3 Results

The juveniles were numerically the dominant component of the cohort and consequently, despite their individually smaller biomass, contributed the greater portion of respiration and production (Table 25). The productivity coefficient of the cohort was 2.3829. Estimated cohort duration was 1464.8 degree-day, with the juveniles and adults each contributing 50% of this time, as the model specifies. This estimate was approximately 33% longer than the observed cohort duration of 1104.8 degree-days. The observed contributions of the juveniles and adults to cohort duration were 44% and 56% respectively.

Seasonal accumulated degree-days above 0°C was greatest in 1973, ranging from 833 degree-days on the raised beach at 0-5 cm depth, to 228 degree-days in the meadow at 5-10 cm depth (Table 26). The equivalent 1972 values were 397 and 42 degree-days.

Cohort duration was greatest in 1972, ranging from 2.5 seasons on the raised beach at 0-5 cm depth, to 23.7 seasons in the meadow at 5-10 cm depth (Table 27). The equivalent 1973 cohort times were 1.2 and 4.4 seasons.

Respiration in 1972 ranged from 7725.9 cal m^{-2} on the raised beach at 0-5 cm depth, to 71.4 cal in the meadow at 5-10 cm depth (Table 28). Respiration was substantially greater in 1973, with 16558.3 cal on the raised beach and 519.6 cal in the meadow at the same depths.

Production resembled respiration in variation with microhabitat and season (Table 28). In 1972 nematodes produced 10683.8 cal of tissue m^{-2} on the raised beach at 0-5 cm depth, and 98.7 cal in the meadow at 5-10 cm depth, while the corresponding 1973 values were 22897.9 and 718.6 cal.

Nematodes dominated invertebrate respiration and production on the raised beach with 85.0% and 86.9% respectively (Table 29). The Enchytraeidae were the next most important group, accounting for 9.0% of respiration, and 7.9% of production. The other groups were relatively unimportant. In the meadow nematodes contributed 25.6% of respiration and 33.5% of production, and were second after the Enchytraeidae in relative importance of their contribution to both respiration and production.

Table 25. Production estimates for the cohort, based on a mean individual dry weight of 0.4297 ug.

Parameter	Juveniles	Adults	Combined
Average no.	295.45	3.17	298.62
Average wt (ug)	0.3553	7.3589	0.4297
Production (ug)	372.8112	275.8074	648.6186
Production (cal)	1.3716	1.0126	2.3842
Respiration (cal)	1.6047	0.1194	1.7241
Cohort time (degree-days)	732.4	732.4	1464.8
Observed cohort time	479.9	624.9	1104.8

Table 26. The 1972 and 1973 accumulated degree-days above 0°C for the raised beach and meadow at 0-5 cm and 5-10 cm soil depth (Courtin and Labine, 1977).

Year	Soil Depth (cm)	Raised Beach	Meadow
1972	0-5	397	103
	5-10	368	42
1973	0-5	833	359
	5-10	788	228

Table 27. The 1972 and 1973 estimates of cohort duration, expressed as seasons per cohort, for the raised beach and meadow at 0-5 cm and 5-10 cm soil depth.

Year	Soil Depth (cm)	Raised Beach	Meadow
1972	0-5	2.5	9.6
	5-10	2.7	23.7
1973	0-5	1.2	2.8
	5-10	1.3	4.4

Table 28. The 1972 and 1973 estimates of nematode seasonal respiration and production in cal m^{-2} for the raised beach and meadow at 0-5 cm, 5-10 cm, and 0-10 cm soil depth.

Year	Soil Depth (cm)	Raised Beach		Meadow	
		Respiration	Production	Respiration	Production
1972	0-5	7725.9	10683.8	606.2	838.3
	5-10	1857.2	2568.3	71.4	98.7
	0-10	9583.1	13252.1	677.6	937.0
1973	0-5	16558.3	22897.9	2408.4	3330.5
	5-10	4490.1	6209.2	519.6	718.6
	0-10	21048.4	29107.1	2928.0	4049.1

Table 29. Nematode mean seasonal respiration and production in cal m^{-2} for the raised beach and meadow, compared with similar information for other important invertebrate taxa (Ryan, 1977a).

Invertebrate Taxon	Raised Beach Respiration	Raised Beach Production	Meadow Respiration	Meadow Production
Rotifera	0.1	0.1	2.6	3.2
Nematoda	15316	21180	1803	2493
Enchytraeidae	1616	1930	2563	3104
Tardigrada	151	193	13.9	18.4
Crustacea	0	0	1076	410
Acarina	106	61	57	35
Araneida	12	23	0.8	1.2
Collembola	552	736	143	107
Lepidoptera	16	13	0	0
Diptera	234	220	1362	1256
Hymenoptera	27	18	35	23
Total	18030	24374	7055	7451

7.4 Discussion

7.4.1 Respiration and Production

The production estimates for the 'synthetic cohort' (Table 25) indicate that juvenile nematodes contribute the greater proportion of cohort production, as might be expected from their numerical dominance. However, the production model incorporates the viable part of adult reproductive effort (i.e. the eggs which hatched) in the juvenile contribution to production and therefore overestimates juvenile production and underestimates the adult contribution. The adults in fact contribute 53% of the nominally juvenile production, and 69% of cohort production in the form of eggs. This large contribution by the adults reflects de Soyza's (1973) findings in her studies on Aphelenchus avenae, in which individual females 'allocated' 68% of production to eggs and 32% to growth during their lives. These data support the expectation that r selected organisms exhibit high reproductive effort in terms of biomass produced (Pianka, 1978).

In view of the large contribution made by the adults to production, their contribution to cohort respiration is relatively small. The adult production and respiration data give a productivity coefficient of 9.4807, compared with the cohort coefficient of 2.3829. While production of eggs is probably very efficient in terms of the amount of energy expended by the eggs in respiration (i.e. the parent takes care of most of the maintenance functions), I believe the adult productivity coefficient is unrealistically high. I noted in Chapter 6 that the function I obtained describing the relationship between respiration and weight obscured the fact of very high respiration rate in large adults. The inadequacy of this function is probably sufficient explanation of the low adult contribution of cohort respiration (I discuss the limitations of the respiration/weight component of the production model in section 7.4.3).

For comparison with my nematode productivity coefficient, I calculated the coefficients for a large number of animals from annual population production and respiration data provided by McNeill and Lawton (1970). For 29 species of comparatively short-lived poikilotherms (mainly small arthropods) the mean productivity coefficient was 1.7389 (range 1.1761-2.8889), for 13 species of long-lived poikilotherms (mainly molluscs and fish) the mean was 1.2371 (range 1.0425-2.1970), and for 13 species of homoiotherms the mean was 1.0262 (range 1.0011-1.1111). Acknowledging that the nematode coefficient is probably high (e.g. if adult respiration were increased, say, 10 times to match adult production, the cohort productivity coefficient would $\simeq$ 1.9), it fits comfortably within the range of coefficients exhibited by other short-lived poikilotherms.

I wish to note here that I expect the productivity coefficients for relatively r selected species of nematodes (e.g. rhabditids) to be higher than the value I obtained for Chiloplacus sp. On the other hand, the coefficients for relatively K selected nematodes (e.g. dorylaimids) are likely to be lower than my value for Chiloplacus sp.

Observed duration of the juvenile stage of Chiloplacus sp. was approximately 430 degree-days above $0^{\circ}C$, compared with 532 degree-days estimated by the model from the unmodified data, and 732 degrees from the modified data (i.e. after being multiplied by 15.9187). The model therefore overestimated cohort duration, and consequently underestimates annual respiration and production. However, assuming that larger species of nematodes take longer to develop than do smaller species, because the average individual size of the field population was larger than the average size of Chiloplacus sp., average field development time is probably longer than that of Chiloplacus sp. Unfortunately I lacked the information necessary to resolve this problem, hence my decision to use observed cohort duration, rather than the model's estimate, for my calculations.

The temperature regimes of 1972 and 1973

(Table 26) demonstrate the striking variation possible in the length of the High Arctic growing season. For example, the raised beach at 0-5 cm depth accumulated more than twice the number of degree-days in 1973 than in 1972, and the 1973 meadow value at 5-10 cm depth was five times the corresponding 1972 figure. The differences in cohort duration between 1972 and 1973 (Table 27) reflect the different temperature regimes of the two seasons.

The consistently shorter within-season cohort times of the raised beach compared with the meadow were caused by the higher temperatures in the raised beach, particularly in 1972, when the raised beach accumulated nearly four times the meadow value at 0-5 cm depth, and nine times at 5-10 cm depth. The greater thermal capacity of the wetter meadow, and shallower active layer (Muc, 1977), accounts for its lower temperatures.

Cohort times were also consistently longer at 5-10 cm depth than in the top 5 cm in both study areas and reflect soil temperature gradients. The gradient was most marked in the meadow, especially in 1972, when the number of degree-days at 5-10 cm depth was only 40% of the number at 0-5 cm depth. The temperature gradient in the meadow, which otherwise conflicts with its relatively high thermal capacity, is explained by the shallower active layer in this habitat.

The 1973 cohort times, and some of the 1972 times, seem reasonable when it is recalled that generation time (of Chiloplacus sp.) is half of the measured cohort time. However, some 1972 meadow estimates are very long, particularly the 23.7 seasons at 5-10 cm depth. Nematodes may live this long, but two considerations suggest that the very long cohort times are misleading. Firstly, the 1972 summer was unusually short, and the 23.7 seasons become 7.4 seasons when the two summers are averaged (1972 and 1973 were the coldest and warmest of the Devon Island project, and the mean of the two years was approximately the mean of the project's five years). In terms of generation time (i.e. for Chiloplacus sp.), these 7.4 seasons become 4.2 seasons. Secondly, the nematodes may regularly migrate vertically through the soil profile, in which case their distribution indicates that they spend most of their lives near the surface where temperatures are highest.

Annual respiration and production, unlike standing crop, are markedly affected by microclimate and, consequently, the estimates for these two parameters are very different for the two years (Table 28). For example, while the 1973 standing crop in the meadow at 5-10 cm depth was 1.2 times the corresponding 1972 value, the equivalent respiration and production estimates were about six times larger. Similarly, while the raised beach average annual standing crop was 3.0 times that of the meadow, annual respiration and production on the raised beach averaged 8.5 times greater than in the meadow. It is evident that for nematodes, in contrast to mammals and waterfowl, meadows located within predominately high arctic communities do not constitute oasis permitting increased levels of productivity and diversity at these latitudes (cf. Bliss, 1977a).

The importance of microclimate in governing nematode respiration is emphasized when my data are compared with similar information from temperate habitats. Wasilewska (1971) obtained nematode standing crops of 431 to 1,507 cal m^{-2} (recalculated assuming 3.679 cal mg^{-1} ash-included substrate, and a dry weight equal to 58.5% of wet weight) in several habitats, and associated annual respiration of 5,700 to 23,500 cal m^{-2}. Banage (1963) estimated nematode standing crops of 1,078 to 1,725 cal m^{-2} (recalculated as above), and annual respiration of 19,800 cal m^{-2}. Phillipson et al. (1977) obtained a standing crop of 172 cal m^{-2}, and respiration of approximately 1432 cal m^{-2} $year^{-1}$. These author's estimates of annual respiration, when compared with my estimates on a unit weight basis, average more than 10 times larger. Arctic nematodes presumably have relatively low annual respiration (and production) because they are active for only a small part of the year, and experience relatively low temperatures when they are active.

The proportionally very large nematode contribution to invertebrate respiration and production on the raised beach presumably reflects their ability to survive very long dry conditions (Cooper and Van Gundy, 1971). This ability doubtless gives nematodes an advantage over groups like the Enchytraeidae and Collembola which generally lack this ability. On the other hand, the relative unimportance of nematodes in the meadow reflects their low biomass, and is probably a consequence of wet soils with low oxygen content.

There is evidence that nematodes may also dominate invertebrate energy flow in hot deserts. For the Mojave Desert, Crawford (1979) cited nematode metabolism of 1160 cal m^{-2} $year^{-1}$. For the same desert, Edney et al. (1976) estimated Collembolan metabolism at 67-76 cal m^{-2} $year^{-1}$, and saprovore Acari annual metabolism at 24.80 cal m^{-2}.

Studies of nematodes in more temperate communities reinforce the evident importance of nematodes in energy flow in the raised beach invertebrate community. For example, Wieser and Kanwisher (1961) found that nematodes accounted for 25-33% of oxygen consumed by the mud of a Massachusetts salt marsh, while Berthet (1964) estimated that nematodes contributed 30% of invertebrate respiration in a Belgian grassland. In other communities nematodes appear much less important. Cragg (1961) found that nematodes contributed approximately 1% of total invertebrate respiration in two Moor House soils, and he concluded that nematodes probably contributed little to energy flow. Similarly, Phillipson _et al_. (1977) estimated that nematodes were responsible for 0.11-0.13% of total soil respiration. Bunt (1954), working on sub-arctic Macquarie Island, estimated that nematodes accounted for only 0.9% of total microfaunal activity in the soil. At Signey Island nematodes contributed 0.008-0.21% (Spaull, 1973d). Evidently the importance of free-living soil nematodes in energy flow varies with the community, and they may be very important in some environments and insignificant in others. My study shows that nematodes are relatively important in many arctic communities, largely because they can survive conditions which appear to suppress other normally abundant invertebrate groups. For the same reasons nematodes may also be relatively important in hot deserts.

7.4.2 Arctic Communities, and Predictions of Nematode and Invertebrate Respiration and Production

On the basis of the data presented in Table 29, I expect High Arctic Polar Semi-deserts to have average annual nematode respiration and production of at least 10,000 cal m^{-2}. I am more hesitant to make predictions for productive and unproductive Polar Deserts. In Chapter 3.4.5 and Chapter 4.4.2 I predicted that these two communities respectively support nematode densities and standing crops of 25% and 2.5% of my estimates for Polar Semi-deserts. The Polar Desert communities probably exhibit proportionally less nematode respiration and production, because they are colder (and drier) than Polar Semi-deserts. This contrasts with the situation in the study site, where the soil becomes progressively warmer from the transition zone to the crest. On the basis of this uncertain rationale, I expect average annual respiration and production in productive Polar Deserts to be less than 2,500 cal m^{-2}, and much less than 250 cal m^{-2} in unproductive Polar Desert. These figures are lower than those I expected for most temperate and tropical communities (in contrast with my expectations for density and biomass), primarily because of the attenuated Polar growing season.

My data suggest that average annual nematode respiration and production in Low Arctic meadows are about

2,000 cal m^{-2}. I consider this value the lower limit (for mesic hummocky meadows - other meadow types will be lower) because meadows presumably become progressively warmer to the South. Respiration and production in all meadow types should progressively increase relative to standing crop as one proceeds south.

Nematodes undoubtedly dominate invertebrate respiration and production in Polar Semi-deserts and Polar Deserts (i.e. $\gg 75\%$), with their relative contribution probably increasing from Polar Semi-desert to unproductive Desert. On the other hand, the nematode contribution in Low Arctic meadows is likely to be no more than 30% in the most favourable hummocky meadows. I expect that as one proceeds southward the nematode contribution in the meadows declines, as easing climatic conditions and increasing proximity to richer southern faunas increase the diversity of species that can inhabit the meadows.

The combined invertebrate data convincingly demonstrate that there is greater invertebrate respiration and production in the Polar Semi-desert than in meadows in the High Arctic, if only because of the overwhelming importance of nematodes in the drier communities. However, following the rationale offered in the previous two paragraphs, at some point to the south invertebrate respiration and production in mesic hummocky meadows will overtake that of the Polar Semi-desert.

7.4.3 Critique of the Ryan and Whitfield Production Model

Several assumptions of the Ryan and Whitfield model warrant critical comment, as do some aspects of my use of the model. Assumptions of particular concern include the following:

(1) An individual member of the synthetic cohort grows over the weight range encompassed by a composite population comprised of several species of different sizes;
(2) During growth weight increases exponentially;
(3) Respiration is related to increasing weight by a single exponential function;
(4) Respiration increases linearly relative to temperature as temperature rises;
(5) Respiration is proportional to production;
(6) The juvenile and adult stages are separated at the point of cessation of growth;
(7) The life span is dependent upon initial cohort size;
(8) The survivorship curve is exponential in form (i.e. Type II - Deevey, 1947); and
(9) The model is deterministic.

Ryan (1977a) assumed that an individual grows over the weight range encompassed by a composite population of several species of different sizes. When a population consists of several species of different sizes, the largest size class consists of adults of the largest species, the smallest size class consists of immatures of the smallest species, and intermediate size classes are heterogeneous assemblages of adults and immatures of several species. In other words, no individual grows over the entire weight range represented by the composite population, and production is overestimated. In contrast to Ryan, I retained the weight relationship between the smallest and largest individuals I observed in Chiloplacus sp., and instead raised both weights equally to obtain the average individual weight I observed in the field. This means that the smallest and largest weight classes found in the field are not accounted for, and both respiration and production are underestimated. Neither procedure is conceptually satisfactory, and both should be considered preliminary responses to complex population phenomena in the face of insufficient data (however I suspect that neither procedure causes serious error in the production estimates). An improvement over both procedures would be to separate the composite field population into a minimum of three "species", two of which should encompass each end of the size range, and all of which are defined and treated as I have done.

The assumption that weight increases exponentially during growth, and then terminates more or less abruptly (Ryan, 1977a), is probably generally valid for holometabolous invertebrates, but is unlikely to be true for ametabolous and hemimetabolous invertebrates (e.g. Enchytraeidae, Collembola, Acarina, Araneida). The exponential curve is inappropriate for Nematoda (e.g. Sohlenius, 1973b) and I found that the weight growth curve of Chiloplacus sp. is better described by the logistic curve. The logistic curve (and sigmoidal curves in general) gives greater production than does the exponential curve for the same initial and final weights. If the growth curves of the invertebrates contributing most to production on the Truelove Lowland are sigmoidal in form, Ryan (1977a) underestimates invertebrate production on the Lowland. The same limitation applies to my estimates of nematode production. One solution to this problem is to develop models incorporating other forms of growth curve, which are rigorously applied to the appropriate organisms.

The assumption that respiration increases exponentially relative to weight is a convenient one that permits easy incorporation of several observed relationships between respiration and weight, including the surface law (i.e. $b = 0.67$) and the weight proportional law (i.e. $b = 1.00$) (von Bertalanffy, 1957). However, more critical recent work on the metabolic rates of different developmental stages of invertebrates show that such relationships are oversimplifications (e.g. Randolph et al., 1975). Similarly, metabolic rates for specific stages need not bear exponential relationships to changing temperature (e.g. Grodzinski et al., 1975). While I obtained a simple exponential relationship for Chiloplacus sp. that is statistically satisfactory, I feel that more critical work would demonstrate a non-linear relationship that would include increased metabolic rates in reproducing adults (Chapter 6.4). Depending upon their purpose, future models may need to incorporate more sophisticated conceptions of the relationship between respiration and weight.

The Ryan and Whitfield model estimates production at a specified average temperature, which implies a linear relationship between physiological functions and temperature over the range of temperatures encountered by the organism (cf. Patten, 1975). In most arctic animals linearity is lost at the low end of the temperature range encountered (cf. Chapter 8). Consequently, the model overestimates population respiration. This problem may be resolved by determining average respiration rate relative to the temperature regime, rather than respiration rate at an average temperature.

The assumption that respiration is proportional to production is acceptable only because of two special conditions of the Ryan and Whitfield model, namely: (1) production in the form of growth, which is restricted to the juvenile stage, is terminated abruptly; and (2) adult respiration is estimated by a submodel of different form to that used for the juveniles. A proportional relationship between respiration and production, in conjunction with any growth curve other than the abruptly terminated exponential curve, has the consequence that as production tends to zero, respiration also tends to zero. In other words, immatures that have temporarily ceased growth (e.g. diapause), or adults that are past reproductive age, also do not respire. This conundrum may be overcome with a more sophisticated function relating respiration to weight as well as to production, when using growth curves whose upper limits are defined by an asymptote.

Separation of the juvenile and adult stages at cessation of growth (i.e. at metamorphosis) is logical for holometabolous insects, but is not satisfactory for many other invertebrates which mature sexually at substantially below final weight (e.g. Collembola - Addison, 1977b; Cladocera - Winberg, 1971). This is generally true of nematodes (e.g. Sohlenius, 1968, 1973a, 1973b; de Soyza, 1973). Chiloplacus sp. began laying eggs at 60% of final weight (Chapter 5.3). If one accepts cessation of growth as the start of the adult stage for animals such as Collembola and Nematoda, the Ryan and Whitfield model overestimates the duration of the juvenile stage and underestimates the adult stage, thereby overestimating production. Alternatively, ending the juvenile stage at sexual maturity omits production represented by adult growth - which was about 5% of cohort production in the case of Chiloplacus sp. Sigmoidal growth curves do not require that the juvenile and adult stages be separated at the point at which growth ceases.

The manner in which the life span is calculated is also questionable. According to the model, the death rate is exponential with respect to degree-day time (Ryan, 1977a). Because the maximum life span is the time until the last member of the cohort dies, the life span is highly dependent upon initial cohort size. In practice, increasing initial cohort size reduces cohort duration (and concurrently, increases cohort production), thereby increasing the field production estimates. Conversely, reducing initial cohort size increase cohort duration, and reduces the field estimates. Cohort duration clearly should not be tied to initial cohort size.

Apart from the conceptual problem involved in determining cohort duration,in practice the model's estimates proved inaccurate. For Chiloplacus sp. I observed a mean generation time of 517.1 degree-days, and a combined juvenile-adult cohort duration of 993.7 degree-days (Chapter 5.3.4). The model's estimate of the duration of the juvenile stage was 531.8 degree-days. When I multiplied the input data by 15.9187, the model's estimate became 732.4 degree-days (Table 25). The errors associated with the model's estimates are large enough to reduce my estimates of population respiration and production by one-third.

The assumption of a constant mortality rate for all stages (i.e. exponential decline, or Type II survivorship curve - Deevey, 1947) simplifies production calculations, but probably is not the most representative survivorship curve for arctic invertebrates. I expect arctic invertebrates generally to be r selected, and to experience relatively high rates of mortality in the early stages, and lowered rates in older individuals. In other words, Type III survivorship curves probably predominate. Type III survivorship curves have a higher proportion of juveniles in the population than do Type II curves, which in turn have a higher proportion of juveniles than do Type I curves. Reduced proportions of adults increase cohort production relative to respiration, i.e. the production coefficients increase. On the basis of this argument, I have probably underestimated nematode production and overestimated respiration, and I expect that Ryan's (1977a) estimates for some of the invertebrates he studied are similarly flawed.

Because the Ryan and Whitfield model is deterministic, confidence limits cannot be put on its estimates, although its sensitivity can be determined by altering the values of the input data. A stochastic version is an obvious next step in the development of the model.

Despite its limitations, I consider the Ryan and Whitfield model a valid and useful research tool. Probably the model's most important limitation is that it describes a special case, to which it should be restricted (i.e. holometabolous insects). This limitation has not been fully recognized by its authors, who have applied the model too generally. Having made this point, I must acknowledge that I have ignored my own recommendation, as I have used the model for nematodes in this thesis. Consequently, I consider my estimates preliminary, although they are an improvement over my earlier estimates (Procter, 1977a). I used the model for two reasons: (1) it is very convenient to use, and (2) there do not appear to be any superior alternatives available (*cf*. Winberg, 1971).

Recognizing that the Ryan and Whitfield model cannot accurately estimate production of all invertebrates, I am developing with a colleague a new production model that better accounts for the range of production processes shown by invertebrates. Because this new model will incorporate von Bertalanffy's (1957) metabolic types, Ricklef's (1967) growth curves, and Deevey's (1947) range of survivorship curves, the model will also be suitable for estimating vertebrate production

Chapter 8

INVERTEBRATE RESPIRATION ON THE TRUELOVE LOWLAND

8.1 Introduction

In this chapter I present information on respiration rates and metabolic rates for representatives of most of the important terrestrial and aquatic invertebrate groups found on the Truelove Lowland. The study included species of Enchytraeidae, Crustacea, Acarina, Collembola, Lepidoptera, Muscidae and Chironomidae. I carried out the field research during July and August, 1972, and from June to September, 1973.

These studies were part of a wider investigation to determine the role of invertebrates in energy flow in this high arctic terrestrial ecosystem. Ryan (1977a) obtained the other information required to estimate invertebrate energy flow, and presented a synthesis of this information.

The information presented in this chapter was not intended to test any of the many questions being asked about metabolic adaptation to cold (e.g. Scholander _et al_., 1953; Hochachka and Somero, 1973; Wieser, 1973). I consider these data valuable primarily because there is very little information on metabolic rates available for invertebrates from High Arctic regions. However, my data do permit some tentative conclusions to be drawn regarding the occurrence of metabolic adaptation in Arctic invertebrates. My data also permit me to compare the metabolic rates of High Arctic nematodes with those of other High Arctic invertebrates at the same temperatures. This will allow me to determine whether nematodes have lower metabolic rates than do most other poikilothermic metazoa, as appears probable in more temperate environments.

8.2 Methods

I measured oxygen consumption at 2°, 7° and 12°C, using the volumetric microrespirometer described by Gregg and Lints (1967). A Haake Unitherm thermoregulator with cooling coil maintained the temperatures within ±0.25°C of the desired levels. Interchangeable chambers of 100, 250 and 800 ul volume accommodated animals of different sizes. The apparatus was sensitive to change in gas volume of 0.0015% hr^{-1}. When individual oxygen consumption was less than this rate, I studied several specimens together to obtain measurable rates.

I collected the experimental animals immediately before experimentation, and allowed them to equilibrate with the system for one hour before taking readings. The animals were not acclimated to experimental temperatures. Six respirometers were operated simultaneously, with one left empty to serve as control for thermal and barometric changes. A minimum of five readings at 30 or 60 min intervals were taken $respirometer^{-1}$ $temperature^{-1}$. I included all readings in the reported results, regardless of level of activity of the animals.

I obtained the dry weights with a Cahn C2 Electrobalance accurate to 0.05 ug, after drying the material for 24 hr at 80°C with calcium chloride.

8.3 Results

Mean metabolic rate for all species at 2°C was 0.5366 ul O_2 mg dry wt^{-1} hr^{-1}, with a range of 1.3690 to 0.1322 (Table 30). At 7°C the mean was 1.1531, and ranged between 2.9549 and 0.2513, and at 12°C the corresponding values were 1.9973, 5.5785 and 0.3066 respectively.

The relation between metabolic rate (R) and body weight (W) for the 16 species at each temperature is represented by the equation:

$$\log R = \log a + b \log W$$

where R is in ul O_2 ind^{-1} hr^{-1}, W is in mg dry wt ind^{-1}, a (O_2 consumption of a 1 mg individual at the specified temperature) is the intercept, and b is the slope of the log-log plot of O_2 consumption in ind^{-1} hr^{-1} versus weight ind^{-1}(Table 31, Fig. 15). Analysis of covariance showed that none of the b-values were significantly different ($P = 0.05$).

The mean Q_{10} value for the 2°-12°C interval was 4.01, with a range of 9.20 to 1.19 (Table 32). The corresponding values at 2°-7°C were 6.86, 27.28 and 1.08, and the 7°-12°C values were 2.99, 7.72 and 1.32. Eleven species had smaller Q_{10} values at 7°-12°C than at 2°-7°C, while five species had larger values at 7°-12°C.

Table 30. Oxygen consumption and dry weight for 16 invertebrate species (n = 5).

Species	°C	Dry wt mg		Oxygen consumption			
				ul O_2 $ind^{-1}hr^{-1}$		ul O_2 $mg^{-1}hr^{-1}$	
		mean ±	SD	mean ±	SD	mean ±	SD
ENCHYTRAEIDAE							
Henlea nasuta	2	0.0371	0.0422	0.0308	0.0319	0.7675	0.2594
	7	0.0310	0.0291	0.0344	0.0326	1.1377	0.6097
	12	0.0336	0.0186	0.0689	0.0417	1.9188	0.5791
CRUSTACEA							
Daphnia pulex	2	0.0430	0.0032	0.0587	0.0186	1.3690	0.4186
	7	0.0441	0.0054	0.1090	0.0193	2.4897	0.4933
	12	0.0432	0.0089	0.2058	0.0248	5.0027	1.4051
Prionocypris glacialis (Sars)	2	0.1239	0.0082	0.0416	0.0074	0.3354	0.0535
	7	0.0755	0.0055	0.0569	0.0150	0.7508	0.1891
	12	0.1125	0.0209	0.1196	0.0214	1.0902	0.2148
Cyclops magnus	2	0.1045	0.0062	0.0410	0.0063	0.3982	0.0628
	7	0.1117	0.0127	0.1480	0.0881	1.3080	0.7390
	12	0.0964	0.0106	0.1497	0.0516	1.5165	0.5483
Cyclops magnus (juvenile)	2	0.0194	0.0022	0.0224	0.0079	1.2026	0.4511
	7	0.0182	0.0015	0.0535	0.0182	2.9549	0.9933
	12	0.0189	0.0042	0.1047	0.0239	5.5785	0.9445
Attheyella nordenskioldii	2	0.0102	0.0005	0.0119	0.0058	1.1632	0.5493
	7	0.0083	0.0011	0.0234	0.0143	2.6927	1.4333
	12	0.0089	0.0008	0.0346	0.0076	3.9691	1.0798

Table 30. Continued.

Species	°C	Dry wt mg		Oxygen consumption			
				ul O_2 ind^{-1}hr^{-1}		ul O_2 mg^{-1}hr^{-1}	
		mean ±	SD	mean ±	SD	mean ±	SD
ACARINA							
Trichoribates polaris Hammer	2	0.0147	0.0007	0.0036	0.0014	0.2436	0.0922
	7	0.0145	0.0008	0.0052	0.0015	0.3589	0.1159
	12	0.0141	0.0008	0.0060	0.0015	0.4254	0.1060
Hermannia subglabra Berlese	2	0.0402	0.0038	0.0059	0.0015	0.1469	0.0342
	7	0.0438	0.0056	0.0108	0.0047	0.2513	0.1123
	12	0.0451	0.0069	0.0144	0.0061	0.3066	0.1059
Lebertia porosa Thor, S. Lat.	2	0.2849	0.0314	0.0446	0.0195	0.1596	0.0735
	7	0.2670	0.0893	0.2063	0.0755	0.8336	0.4114
	12	0.3157	0.0649	0.3612	0.1305	1.1912	0.4978
COLLEMBOLA							
Hypogastrura sp. nr *trybomi* (Schott)	2	0.0188	0.0034	0.0052	0.0028	0.2732	0.2509
	7	0.0255	0.0081	0.0172	0.0066	0.6953	0.2436
	12	0.0166	0.0052	0.0168	0.0102	1.1960	1.0317
Folsomia agrelli Sisin	2	0.0025	0.0001	0.0003	0.0011	0.1322	0.4766
	7	0.0034	0.0004	0.0021	0.0010	0.5708	0.2869
	12	0.0042	0.0006	0.0050	0.0033	1.2164	0.8730
LEPIDOPTERA							
Gynaephora rossi (Curtis) (larvae)	2	0.2109	0.0610	0.0714	0.0190	0.3536	0.1079
	7	0.1814	0.0091	0.1506	0.0609	0.8319	0.3373
	12	0.1837	0.0051	0.4250	0.1098	2.3117	0.5873

Table 30. Continued.

Species	°C	Dry wt mg		Oxygen consumption ul O_2 ind^{-1}hr^{-1}		ul O_2 mg^{-1}hr^{-1}	
		mean ±	SD	mean ±	SD	mean ±	SD
MUSCIDAE							
Spilogona prob. *tundrae* Schnabl. (larvae)	2	2.9590	0.1889	1.3737	0.5012	0.4643	0.1666
	7	3.6520	0.7211	1.7687	0.7232	0.4817	0.1851
	12	3.5752	0.4102	2.0021	1.1566	0.5544	0.3124
CHIRONOMIDAE							
Psectrocladius sp. (larvae)	2	0.4829	0.0754	0.2966	0.0847	0.6230	0.1854
	7	0.5605	0.0915	0.7966	0.4126	1.4126	0.6748
	12	0.4440	0.0321	1.0759	0.4266	2.4010	0.9053
Procladius culiciformis (Linné) (larvae)	2	0.5831	0.0768	0.2834	0.1065	0.4791	0.1396
	7	0.3965	0.1636	0.3137	0.2212	0.7975	0.4338
	12	0.4378	0.2550	0.8280	0.4131	1.9026	0.7194
Cricotopus sp. (larvae)	2	0.4597	0.0692	0.2798	0.0832	0.6218	0.2061
	12	0.4920	0.0409	1.0675	0.6579	2.1999	1.3752
Orthocladius sp. (larvae)	2	0.1072	0.0203	0.0412	0.0089	0.3900	0.0866
	7	0.0785	0.0129	0.0656	0.0304	0.8687	0.4403
	12	0.0982	0.0292	0.1103	0.0510	1.1278	0.5228

Table 31. Relation between oxygen consumption (R) and dry weight (W) for 16 invertebrate species at 2°, 7° and 12°C; $\log R = \log a + b \log W$.

Temp (°C)	a	± 95% CI	b	± 95% CI
2	-0.3290	0.2957	1.0427	0.2232
7	-0.1143	0.2995	0.9343	0.2182
12	0.1160	0.3175	0.9463	0.2404

Table 32. Q_{10} values for 16 invertebrate species at three temperature intervals.

Species	2°- 12°C	2°- 7°C	7°- 12°C
Henlea nasuta	2.50	2.20	2.84
Daphnia pulex	3.65	3.31	4.04
Prionocypris glacialis	3.25	5.01	2.11
Cyclops magnus	3.92	10.79	1.43
Cyclops magnus (juvenile)	4.64	6.04	3.56
Attheyella nordenskiodlii	3.41	5.36	2.17
Trichoribates polaris	1.75	2.17	1.40
Hermannia subglabra	2.09	2.93	1.50
Lebertia porosa	7.46	27.28	2.04
Hypogastrura sp.	4.38	6.48	2.96
Folsomia agrelli	9.20	18.64	4.54
Gynaephora rossi	6.54	5.54	7.72
Spilogona tundrae	1.19	1.08	1.32
Psectrocladius sp.	3.85	5.24	2.83
Procladius culiciformis	3.97	2.77	5.69
Cricotopus sp.	3.54	-	-
Orthocladius sp.	2.89	4.96	1.69
Mean	4.01	6.86	2.99

Table 33. Respiration rates for some arctic, antarctic and alpine invertebrates. For the following species the associated percentages were used to convert live weight to dry weight: C. antarcticus, 30%; H. tulbergi, 29.9% (Addison, 1977b); F. regularis, 35%; O. groenlandicus, 35%; Z. exulans, 18.93% (Hågvar and Østbye, 1974); T. excisa, 25%.

Species	Temperature (°C)	Dry wt mg	ul O_2 $mg^{-1}hr^{-1}$	Reference
CRUSTACEA				
Cyclops vernalis (copepodite IV,	0	0.0025(IV)	1.1204	Taube-Nauwerck, 1972.
adult ♀)	0	0.0059(♀)	0.7705	
Limnocalanus macrurus	0	0.012-0.028	1.3490	Roff, 1973.
	2	0.012-0.028	1.5091	
	4	0.012-0.028	1.8436	
	10	0.012-0.028	2.6545	
	15	0.012-0.028	4.1564	
Mysis relicta	0	0.08-4.50	0.9526	Lasenby and Langford, 1972.
	2	0.08-4.50	1.0647	
	4	0.08-4.50	1.4149	
	6	0.08-4.50	1.6881	
	8	0.08-4.50	1.8562	

Table 33. Continued.

Species	Temperature (°C)	Dry wt mg	ul O_2 $mg^{-1}hr^{-1}$	Reference
COLLEMBOLA				
Cryptopygus antarcticus (Sizes: I, II, III, IV, V)	2	0.0009(I)	1.404	Tilbrook and Block, 1972.
		0.0031(II)	0.836	
		0.0077(III)	0.564	
		0.0158(IV)	0.416	
		0.0278(V)	0.328	
	6	I	5.520	
		II	2.024	
		III	0.956	
		IV	0.532	
		V	0.336	
	10	I	16.108	
		II	4.920	
		III	2.012	
		IV	1.008	
		V	0.588	
Hypogastrura tulbergi	10		0.7448	Addison, 1977b.
Folsomia regularis	10		0.8731	Addison, 1977b.
Onychiurus groenlandicus	10		0.3391	Addison, 1977b.

Table 33. Continued.

Species	Temperature (°C)	Dry wt mg	ul O_2 $mg^{-1}hr^{-1}$	Reference
LEPIDOPTERA				
Zygaena exulans (larvae)	5	2.5-52.0	0.4437	Hågvar and Østbye, 1974.
	10	2.5-52.0	0.9667	
	15	2.5-52.0	1.8542	
	20	2.5-52.0	2.3930	
TIPULIDAE				
Tipula excisa (larvae: II, III, IV)	5	2-6(II)	0.82	Hofsvang, 1972; Hofsvang, 1973.
	10	2-6(II)	1.14	
	20	2-6(II)	1.75	
	5	6-16(III)	0.44	
	10	6-16(III)	0.80	
	15	6-16(III)	1.30	
	20	6-16(III)	1.44	
	5	16-41(IV)	0.26	
	10	16-41(IV)	0.38	
	15	16-41(IV)	0.66	
	20	16-41(IV)	0.82	
Pedicia hannai	0.5	0.1-8.0	0.491	MacLean, pers. comm.
	5	0.1-8.0	0.655	
	10	0.1-8.0	1.311	
	15	0.1-8.0	1.886	
	20	0.1-8.0	2.582	

Table 33. Continued.

Species	Temperature (°C)	Dry wt mg	ul O_2 $mg^{-1}hr^{-1}$	Reference
CHIRONOMIDAE				
Pseudodiamesa sp.	0	0.002-2.487	1.708-0.136	Welch, 1976.
Lauterbornia sp.	0	0.0002-0.926	0.222-0.219	Welch, 1976.
Heterotrissocladius sp.	0	0.001-0.726	0.600-0.115	Welch, 1976.
Trissocladius sp.	0	0.0003-0.499	1.429-0.234	Welch, 1976.
Orthocladius sp.	0	0.0004-0.693	1.463-0.264	Welch, 1976.
Chironomus sp.	5	0.30(III)	0.37	Bierle, 1972.
(larvae: III, IV)	10	0.30(III)	0.67	
	15	0.30(III)	1.18	
	20	0.30(III)	1.72	
	25	0.30(III)	2.28	
	5	1.90(IV)	0.20	
	10	1.90(IV)	0.34	
	15	1.90(IV)	0.70	
	20	1.90(IV)	0.94	
	25	1.90(IV)	1.30	

Table 34. Q_{10} values for some arctic, antarctic and alpine invertebrates.

Species	Temperature Interval (°C)	Q_{10}	Reference
Limnocalanus macrurus	0-4	2.18	Roff, 1973.
	4-10	1.84	
	10-15	2.45	
Mysis relicta	0-4	2.69	Lasenby and Langford, 1972.
	4-8	1.97	
Cryptopygus antarcticus Sizes: I, II, III, IV, V.	2-6	30.65, 9.12, 3.74, 1.85, 1.06	Tilbrook and Block, 1972.
	6-10	14.55, 9.21, 6.43, 4.94, 4.05	
Zygaena exulans (larvae)	5-10	4.75	Hågvar and Østbye, 1974.
	10-15	3.68	
	15-20	1.67	
Tipula excisa Instars: II, III, IV.	5-10	1.93, 3.31, 2.14	Hofsvang, 1973.
	10-15	- 2.64, 3.02	
	15-20	- 1.23, 1.54	
Pedicia hannai (larvae)	0.5-5	1.90	MacLean, pers. comm.
	5-10	4.01	
	10-15	2.07	
	15-20	1.87	
Chironomus sp. Instars: III, IV.	5-10	3.27, 2.89	Bierle, 1972.
	10-15	3.10, 4.24	
	15-20	2.12, 1.80	
	20-25	1.76, 1.91	

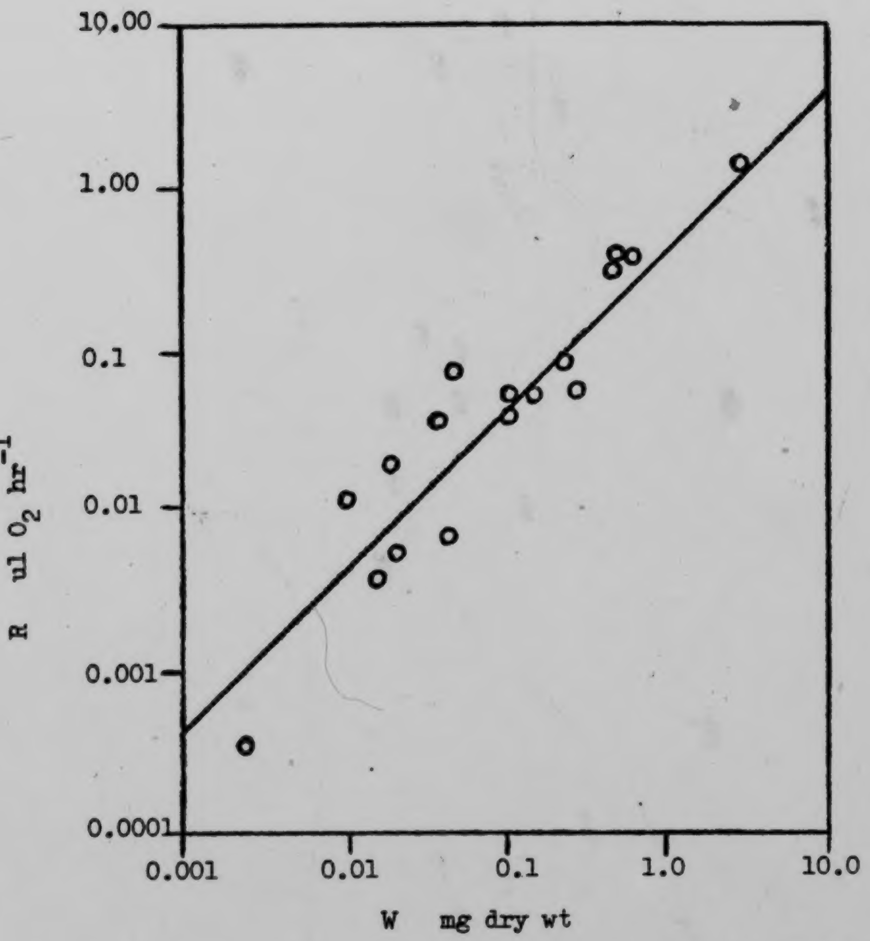


Fig. 14. Relationship between respiration rate (R) and body weight (W) for 16 invertebrate species at 2°C. Respiration equation: $\log R = -0.3290 + 1.0427 \log W$.

8.4 Discussion

In the present study the Crustacea had the highest metabolic rates, followed by the Enchytraeidae, Lepidoptera and Chironomidae (Table 30). The reproductive condition of two of the crustacean species probably contributed to their high metabolic rates. For example, the *Daphnia pulex* individuals were all females with eggs, as were some of the *Attheyella nordenskioldii* specimens. Developing eggs may have increased metabolic rate while contributing relatively little to biomass. Webb (1969) reported that *Nothrus silvestri* (Acari) adults containing developing eggs had a weight-specific metabolic rate 56% greater than that of non-breeding adults. The inclusion of juvenile *Cyclops magnus*, which metabolised at approximately three times the rate of the adults, also contributed to the high average metabolic rate.

The two terrestrial mites, *Trichoribates polaris* and *Hermannia subglabra*, had very low metabolic rates at all temperatures, although both collembola species and the aquatic mite *Lebertia porosa* had equally low rates at 2°C, and *Spilogona tundrae* metabolised nearly as slowly at 12°C (Table 30). Webb (1970) reported that oribatid mites have lower metabolic rates than most other soil-dwelling invertebrates, including the Enchytraeidae and Collembola. The present study supports this general relationship, but differs in that both collembolan species metabolised more slowly than the one enchytraeidae studied. The low metabolic rates of the oribatid mites probably reflect their sedentary habits (Webb, 1970).

Published crustacean metabolic rates resembled my data in being relatively high, particularly at 0° and 2°C (Table 33). The Crustacea metabolized more rapidly at these temperatures than did most other species at 5° and 10°C. The exceptions are the smallest individuals of the collembolan Cryptopygus antarcticus (Tilbrook and Block, 1972), and the very early instar chironomid larvae (Welch, 1976), almost all of which had similar rates to the crustacea at the lowest temperatures. Cryptopygus antarcticus also metabolised more rapidly than the crustacea at higher temperatures.

Juvenile C. antarcticus provide the greatest contrast to my data. For example, C. antarcticus weighing 0.0031 mg metabolised at approximately 5 times the rate of adult Folsomia agrelli of the same weight. On the other hand, adult C. antarcticus metabolised much more slowly, at a rate similar to adult Hypogastrura of the same size. Cryptopygus antarctucus provides a striking example of the size-specific differences in metabolic rate frequently observed between developmental stages (e.g. Bierle, 1972; Hofsvang, 1973; Welch, 1976). From my study Cyclops magnus shows the same phenomenon.

Apart from C. antarcticus, collembola from other studies differed little from the species I studied. Addison (1977b) obtained metabolic rates for Hypogastrura tulbergi and Folsomia regularis at 10°C that are intermediate between the 7° and 12°C rates I obtained for Hypogastrura sp and Folsomia agrelli. Onychiurus groendlandicus metabolised more slowly than the other species.

Published information for chironomids shows the same size-specific differences in metabolic rate reported for the collembolan C. antarcticus (Welch, 1976; Bierle, 1972). Consequently, the early instar chironomids metabolised much more rapidly than the later instars, including the final instar larvae I studied. However, my data are comparable to the information obtained by Welch for larvae of equivalent development.

In general the metabolic rates I obtained are comparable to data for other arctic, antarctic and alpine invertebrates at similar temperatures. I attribute the few major differences to studies of different developmental stages, and possibly to different methodology.

Chiloplacus sp. had a metabolic rate at 2°C that was only slightly lower than the average value for the invertebrates in general (i.e. 0.275×10^{-3} ul O_2 ug^{-1} hr^{-1}, compared with 0.349×10^{-3} ul). Because of its lower weight exponent, Chiloplacus sp. necessarily has relatively lower metabolic rates compared to the invertebrates at temperatures above 2°C. However, the nematode fauna as a whole had a metabolic rate of 0.052×10^{-3} ul at 2°C, that is, only one-seventh of the average rate of the other invertebrates. These results confirm my expectation that nematodes have lower metabolic rates than do more highly evolved invertebrate poikilotherms.

With all three weight/oxygen consumption exponents close to unity, I concluded that oxygen consumption is directly proportional to weight when species are compared (Table 31, Figure 15). Scholander et al. (1953) obtained exponents of 0.80-0.85 and likewise concluded that metabolic rate is directly proportional to weight. In contrast, when different developmental stages of single species were compared, only two cases of direct proportionality were observed - Lauterbornia sp. (Welch, 1976), and Henlea nasuta in the present study. In the other species oxygen consumption increased more slowly than weight (e.g. C. antarcticus, T. excisa, C. magnus, and most chironomid larvae).

The variety of apparently species-specific weight/respiration exponents in the literature has resulted in several hypotheses, including the "direct proportionality" relationship illustrated by several species I studied, and the "surface law" relationship (cf. Chapter 6). However, Keister and Buck (1973) suggested that because of the number of variables which may affect both metabolic rate and weight, exponents should be considered descriptive only. By contrast, I tried to show in Chapter 6 why one may expect a variety of exponents among invertebrates.

The three mean Q_{10} values are similar to the corresponding values estimated from Krogh's (1941) standard metabolic curve (Table 32). However, the means approximate the standard curve primarily because of several very large values, and most of my values are smaller than the standard, including three between 1.19 and 2.09 at 2°-12°C, and three between 1.08 and 2.20 at 2°-7°C.

Most species had decresing Q_{10} values with increasing temperature, indicating a trend toward linear rather than exponential increase in metabolic rate with increasing temperature. Two species, Henlea nasuta and Spilogona tundrae, had nearly constant values, denoting exponential increase in metabolic rate with temperature, while others, notably Daphnia pulex, Gynaephora rossi and Procladius culiciformis, had increasing Q_{10} values with temperature, and consequently a steeper than exponential rise in metabolic rate.

Stroganov (1956) presented evidence, based on temperature acclimation in fish (Gambusia), that metabolic rate-temperature curves may be more complex than Krogh's standard curve. An important part of Stroganov's thesis is the presence of a 'zone of relative thermoneutrality' in which Q_{10} is relatively low, and which represents the temperature zone to which the organism is acclimated, or in which it usually lives (Duncan and Klekowski, 1975). If Stroganov's curve is widely applicable as Wieser (1973) suggests, the several patterns of Q_{10} values I obtained may indicate that measurements were made at different points on the various curves. For example, only the upper part of the 'zone of thermoneutrality' was covered by the measurements for _Procladius_ _culiciformis_, only the lower part of the zone was included for _Lebertia_ _porosa_, and all three measurements fell within the zone for _Spilogona_ _tundrae_ (Table 32). Aquatic invertebrates presumably have their 'zones of thermoneutrality' at lower temperatures than do terrestrial invertebrates, because the former generally are subject to lower temperatures when active.

While Stroganov's thesis offers an explanation for the variety of my observations, it must be pointed out that measurement at only three temperatures provides insufficient information to determine the form of a complex metabolic rate-temperature curve. Furthermore, none of the studies cited provide sufficient information for reliable analysis of such a curve, which may require 15-20 measurements taken at 1°-2° intervals.

Published Q_{10} values varied between 30.65 at 2°-6°C for immature Cryptopygus antarcticus, and 1.06 at 2°-6°C for adult C. antarcticus (Tilbrook and Block, 1972) (Table 34), showing the same very wide range that I obtained (Table 32). Furthermore, the distribution of values was similar, including a large proportion of relatively small values, and a few very large values. The trends in Q_{10} also resembled my results, with most species exhibiting decreasing Q_{10} values with increasing temperature, while a few had constant or increasing values. Of special interest are the low Q_{10} values for Limnocalanus macrurus, Mysis relicta, Cryptopygus antarcticus (sizes IV & V), Tipula excisa and Pedicia hannai in the 0°-10°C range. These values reinforce my observations that some species habitually living in cold climates have low Q_{10} values. Also noteworthy is the extent to which some of these values, both high and low, diverge from Krogh's standard curve. For example, the Q_{10} values for C. antarcticus stages I & V at 2°-6°C were 30.65 and 1.06 respectively, compared with 8.34 from Krogh's curve. These observations, like those from my experiments, demonstrate that Krogh's curve does not reliably predict invertebrate species-specific metabolic rates at low temperatures.

Scholander et al. (1953) suggested invertebrates may have three methods of adaptation to arctic environments:

(a) low Q_{10}, whereby temperature sensitivity is low; (b) shift of metabolic curve to maintain high metabolic rate; and (c) selection of favourable microclimates.

Scholander *et al.* (1953) found no low Q_{10} values in the arctic invertebrates they studied and concluded that this type of temperature adaptation is more likely to occur in temperate animals, which experience greater temperature variation. I observed low Q_{10} values fairly frequently in both aquatic and terrestrial arctic invertebrates. Although arctic environments, and particularly aquatic environments, experience more constant temperatures than temperate or alpine habitats, relatively small temperature changes can be important because temperatures are often only marginally favourable for life cycle processes. Low Q_{10} values may help maintain adequate metabolic rates in these environments.

Scholander *et al.* (1953) found shifting of metabolic curves only in aquatic invertebrates, which showed relatively high metabolic rates compared to tropical species at low temperatures (they did not measure metabolic rates of tropical species at low temperatures but extrapolated according to Krogh's curve). Scholander *et al.* (1953) did not suggest why modified metabolic curves should be restricted to aquatic invertebrates. However, arctic aquatic environments are undoubtedly colder than terrestrial environments. For example, the wet meadows proved colder than the drier beach ridges (Courtin and Labine, 1977). Furthermore, the high specific heat of water causes temperature to vary less and aquatic animals therefore have access to a smaller range of microclimates than do terrestrial animals. Consequently, aquatic species may require modified metabolic curves in order to attain metabolic rates comparable to those of terrestrial species.

My general studies produced no unequivocal cases of shifting of metabolic curves. For example, Daphnia pulex had a metabolic rate of 2.4897 ul O_2 mg^{-1} hr^{-1} at 7°C, compared with Richman's (1972) 1.8621 ul for similar sized individuals reared at 20° (20° data converted to 7° according to Winberg, 1971). These results do not support the five-fold difference Scholander *et al*. (1953) reported. Lasenby and Langford (1972) compared metabolic rates of the crustacean Mysis relicta from an arctic and a temperate lake and obtained no evidence of metabolic adaptation in the arctic population. Holeton (1974) also found little sign of modified metabolic curves in arctic fish, and showed that some reported examples of cold compensation in arctic fish are questionable on methodological and interpretative grounds. Consequently, while modified metabolic curves appear adaptive, particularly in aquatic species, the evidence for such adaptation is equivocal at best.

Both Chiloplacus sp., and the Truelove Lowland nematode fauna as a whole, showed signs of shifting of the metabolic curve relative to nematodes of more temperate environments (cf. Chapter 6.4). The apparent adaptation of their curves showed as higher metabolic rates below 10°C. Cooper and Ferguson (1973) experimentally demonstrated cold-acclimation of oxygen consumption in two species of free-living nematodes at 10°C relative to 20°C. Nematodes are perhaps atypical for arctic invertebrates in being essentially aquatic organisms that are exploiting the terrestrial environment.

Many of the species studied showed little sign of adaptation of metabolic rate to cold. Lacking adaptation of metabolic rate, these species may have behavioural adaptations which, however, are probably suppressed by the experimental conditions. For example, behavioural thermoregulation of the kind observed in arctic Lepidoptera (Kevan and Shorthouse, 1970) would not occur during conventional respirometry. In the present study two species with high Q_{10} values, Folsomia agrelli and Gynaephora rossi, are active terrestrial animals which can probably locate favourable microclimates very quickly. Thermoregulatory behaviour, including the ability to select favourable microclimates, is presumably shared by all invertebrates and is probably the predominant 'arctic' adaptation to cold

(Scholander *et al.*, 1953). In other words, many arctic species probably lack special metabolic adaptations and, using normal capacity for selecting favourable microclimates, are opportunistic in their utilization of arctic environments.

Chapter 9

EVOLUTIONARY TRENDS IN SPECIES PRODUCTION STRATEGIES, AND THEIR IMPLICATIONS FOR COMMUNITY AND ECOSYSTEM PRODUCTION EFFICIENCIES

9.1 Introduction

Several general questions about efficiencies in energy processing by individuals, populations and communities have been posed in the past (e.g. Lindeman, 1942; Engelman, 1966; Kozlovsky, 1968). We are now beginning to obtain sufficient information to answer some of these questions. For example, increasing numbers of studies on the energetics of individuals are defining the roles of such diverse properties of living organisms as age, thermoregulation, and trophic position in governing gross and net production efficiencies (e.g. Randolph *et al.*, 1975; McNeill and Lawton, 1970; Van Hook, 1971).

With sufficient knowledge of how individual energetic properties vary with the age and reproductive condition of the organism, this information can be integrated into populations through age-specific birth and death rates, and age structure. This makes possible simulation of population energy flow from individual data (Randolph *et al.*, 1975).

In this chapter I use present knowledge of the energetics of individuals and their population characeristics to go beyond simulation of population energy flow, to refine expectations about energy utilization in different trophic levels, communities and ecosystmes. To accomplish this I first integrated different organisms and their populations into the concepts of r and K strategists (MacArthur and Wilson, 1967). I then integrated the populations thus defined into the concepts of 'r selected' and 'K selected' trophic levels, communities and ecosystems. From this base I then predicted the relative performances of these higher levels of ecological organization in terms of efficiencies of energy utilization.

An essential part of this chapter are my predictions for High Arctic and Low Arctic communities, which are set within the framework of my more general predictions.

Finally, I address the last question posed in Chapter 1 - "What is an Arctic insect?", which I have expanded to encompass all invertebrates - in terms of the concepts discussed in this chapter.

9.2 Production Strategies in Animals

During evolution from unicellular animals to metazoa, and from poikilotherms to homoiotherms, an increase in potential population growth rate occurred (Fenchel, 1974; Christiansen and Fenchel, 1977). Thus, a poikilotherm metazoan has a value of r that averages about twice that of a protozoan of similar size, and a homoiotherm metazoan has an r-value averaging about 1.7 times higher than that of a poikilotherm metazoan of the same size (Fenchel, 1974). However, evolution of metazoa also led to higher metabolic rates, presumably because more complex structure and homoiothermy require more energy for maintenance (Fenchel, op. cit.). For example, poikilotherm metazoa have a metabolic rate which averages 8.3 times higher than that of unicellular organisms of the same size (Fenchel, 1974; Hemmingsen, 1960; Zeuthen, 1947). (Nematodes fall between unicellular organisms and most poikilotherms in metabolic rate - Chapter 6.4.1.) Similarly, when poikilotherm and homoiotherm metazoans of identical size are compared, the latter have a metabolic rate which is 28 times higher than that of the former. The smaller slope of the r-body weight relationship (-0.275) relative to that of the metabolic rate - body size relationship (-0.249) found by Fenchel (1974) also indicates that with increasing size an increasing proportion of energy is allocated to maintenance.

Fenchel (1974) proposed that r can be used as a measure of potential population production. Accepting Fenchel's arguments, his data show that the ratio "production/metabolic rate" is about 16.5 (28/1.7) times higher for poikilotherm metazoa than for homoiotherms, and about 4.15 (8.3/2) times higher for unicellular animals than for poikilotherm metazoa. (The "production/metabolic rate" ratio of nematodes will lie between those of unicellular organisms and most poikilotherms.). McNeill and Lawton (1970) compared annual production and respiration data for field populations of different metazoans, and found that while poikilotherm respiration averaged approximately 2.3 times production, respiration of homoiotherms averaged about 55 times their production. In other words, the ratio between population productivity and respiration of poikilotherms is about 23 times larger than that of homoiotherms.

Fenchel's (1974) calculations, based on laboratory data, undoubtedly underestimate the differences in the ratio "production/metabolic rate" between unicellular animals, poikilotherm metazoa and homoiotherm metazoa, as comparison with McNeill and Lawton's (1970) field population data suggests. Consideration of the form of the survivorship curve may explain this shortfall. A population of an animal with a Type III survivorship (Deevey, 1947) will have a relatively high production/metabolic rate ratio, because of the small proportion of the population reaching old age, at which stage little or no energy goes to production, and a large proportion goes into maintenance. Conversely, a population of an animal with a Type I survivorship curve will have a relatively low production/metabolic rate ratio because a relatively large proportion of individuals reach and continue in adulthood. Accepting that unicellular animals are relatively r selected, this supposes Type III survivorship curves (Margalef, 1958; Pianka, 1978). On the other hand, homoiotherms metazoa are relatively K selected, and consequently have Type I survivorship curves. Consequently, the form of the survivorship curve probably substantially increases the differences predicted by Fenchel in the ratio production/metabolic rate between populations of the three kinds of animals.

The differences between populations of poikilotherm metazoa and homoiotherm metazoa may be expressed in terms of population productivity coefficients, as I have done with McNeill and Lawton's (1970) data in Chapter 7.4.1.

9.3 Production Strategies in Plants

Plants show a decline in population/respiration rate ratios with increasing size and structural complexity that is analogous to that demonstrated in animals. In the single-celled planktonic alga Chlorella, the photosynthetically active organs (chromatophores) take up about half of the volume of the protoplasm (Larcher, 1975). Proceeding through annual herbs, perennial herbs, to trees, progressively greater portions of the total plant mass are accounted for by purely respiratory tissues (e.g. stems, roots). For example, in Alpine grassland plants about 70% of total mass is accounted for by purely respiratory tissues; in dwarf ericaceous shrubs of heath and tundra the proportion is 80-90%; and in evergreen trees of tropical and subtropical forests the proportion is about 98% (Larcher, op. cit.). Furthermore, the proportion of purely respiratory organs increases as individual plants mature. This is most marked in the large, highly differentiated trees where, in the first years of life, leaf mass can constitute up to half of the overall biomass of the tree, but comprises only 1-5% of the mass of mature trees (Larcher, op. cit.).

Because the proportion of respiratory tissues increases with increasing size and complexity of the plants the productivity coefficient progressively decreases with increasing size. In populations of autotrophic plankton and in meadows the coefficients may be close to 10 (i.e. 10% of gross production metabolized in respiration), in Beech wood about 2.2 (i.e. 55% production, 45% respiration), and in tropical rain forest about 1.3 (i.e. 22% production, 78% respiration) (Larcher, 1975). Likewise, young plants presumably have larger productivity coefficients than do mature individuals, with the differences in coefficients between young and adult plants probably being least in the simplest plants, and greatest in the most complex plants.

Production of autotrophic single-celled organisms is utilized primarily in reproduction (Larcher, 1975), rather than for maintenance like the large tropical trees at the other end of the complexity continuum. Harper, Lovell and Moore (1970) point out that because annual herbs, perennial herbs, and trees allocate progressively smaller fractions of their resources to reproduction, they constitute progressively more K selected life forms. Assuming, as I did for animals, that r selected unicellular plants have Type III survivorship curves, and that K selected trees tend towards Type I curves, the difference in productivity coefficients between r selected and K selected plants would likewise be increased when their populations are compared.

9.4 Efficiency of Energy Utilization by Species

Several predictions regarding production efficiency can be drawn from the relationships between size, structural complexity, metabolic rate and reproductive strategies I have outlined above. Firstly, r selected organisms not only have relatively high productivity (e.g. Gadgil and Solbrig, 1972), but they also have high production efficiences (e.g. high productivity coefficients). Secondly, K selected organisms have both relatively low productivity (e.g. Pianka, 1978), and low production efficiences. My proposals conflict with the commonly held expectations that r strategists maximize productivity but not efficiency, while K strategists maximize efficiency but not productivity (e.g. MacArthur and Wilson, 1967; Gadgil and Solbrig, 1972; Pianka, 1978). In support of the commonly held expectations, Gadgil and Solbrig (op. cit.) suggested that r selected animals waste more food than do K selected animals when food is abundant. Whether true of not, this possibility does not obscure the underlying physiological superiority of r selected organisms in production efficiency.

While I consider it virtually axiomatic that K selected organisms are less efficient than r selected organisms in production, it may also be axiomatic that K selected organims ultimately gain in the elaboration of superior competitive attributes, whether structural, physiological or behavioural, that result from different utilization of gross production. For example, the great expenditure of energy on supporting tissues by woody plants eventually procures decisive competitive advantages over herbaceous plants in areas with long production periods, as the herbs are slowly but surely overshadowed by the taller woody plants (Larcher, 1975.).

9.5 Efficiency of Energy Utilization by Trophic Levels

Lindeman (1942) offered a relationship between efficiency of energy utilization and trophic level, to quote:

> "Considering that predators are usually more active than their herbivorous prey, which are in turn more active than the plants upon which they feed, it is not surprising to find that respiration with respect to growth in producers (33 per cent), in primary consumers (62 per cent) and in secondary consumers (> 100 per cent) increases progressively. These differences probably reflect a trophic principle of wide application: the percentage loss of energy due to respiration is progressively greater for higher levels in the food cycle."

Modern ecological theory offers another perspective from which to view efficiency of energy utilization by trophic levels: any trophic level in which r selected organisms dominate production will have greater productivity coefficients than will trophic levels which are dominated by K selected organisms. For example, the autotroph level when dominated by unicellular algae, will have a larger coefficient than when dominated by tropical rain forest trees. This relationship should hold regardless of the position of the trophic level in the food chain, and thereby constitutes an important qualification of Lindeman's (1942) trophic principle that "the percentage loss of energy due to respiration is progressively greater for higher levels in the food cycle". For example, the decomposer level, being generally comprised of more r selected organisms than are the immediately preceeding trophic levels, undoubtedly exhibits a larger productivity coefficient than do the preceeding levels. The parasitic level will likewise have a larger coefficient than the preceeding level.

9.6 Efficiency of Energy Utilization by Communities and Ecosystems

Extending the rationale I applied to trophic levels to include communities and ecosystems, those systems in which r selected organisms predominate will also have higher production efficiencies than do systems in which K selected organisms predominate. Larcher (1975) presented information on mean annual energy fixed by gross primary production, and net primary production for different plant communities, from which I calculated annual community productivity coefficients. Listed in order of decreasing annual gross production, the communities and their coefficients are: tropical rain forests, 1.49; winter-deciduous forests, 2.84; sclerophyllous woodland, 2.86; boreal coniferous forests, 2.85; tropical grassland, 5.00; temperate grassland, 7.67; ocean coastal zones, 9.00; open ocean, 9.57; and semi-deserts, 7.00. These data show a striking correlation between the incidence of r selected plants and the size of the productivity coefficient, with the grass-dominated communities having much higher coefficients than the tree-dominated communities, and the autotrophic plankton-dominated communities in turn having still higher coefficients.

A feature of the information on community production presented by Larcher (1975) is that both efficiency of annual radiation utilization via gross production, and amount of gross production, are inversely correlated with the productivity coefficients of these communities. Acknowledging that the first two parameters are important indicators of the performance of communities and ecosystems in energy utilization, my exposition establishes the productivity coefficient as another perspective from which to assess the performance of such systems. Clearly, unproductive and inefficient systems from one point of view may be relatively productive and efficient from another point of view.

9.7 Efficiency of Energy Utilization and Seasonal Succession, Community Succession, and Community Evolution

In order to complete the framework within which I wish to consider Arctic communities, I shall briefly consider temporal changes in efficiency of energy utilization.

Communities subject to unstable and unpredictable climates are likely to be comprised of relatively r selected organisms (e.g. Pianka, 1978). On the other hand, communities subject to stable climates (i.e. which change little with the seasons) are probably comprised of relatively K selected organisms. However, communities subject to temporally variable but predictable climates, probably have a mixture of r and K selected organisms, which show temporal succession. In temperate zones, early spring biomass is relatively low in the community as a whole, and there is little competition for light, water, etc. Later in the season biomass increases, and competition increases as a consequence. Gadgil and Solbrig (1972) found that early spring is a time when annual plants are relatively r selected, and later in the season they become progressively more K selected. On this basis, I suggest that "spring" communities have relatively high productivity coefficients, although efficiencies of radiation utilization via gross production are probably relatively low.

Conversely, "summer" communities will have lower productivity coefficients, and higher efficiencies of radiation utilization.

Community succession has been considered in terms of thermodynamics and r and K selection by Margalef (e.g. 1963) and Odum (1969). "Immature" communities are distinguished from "mature" communities by higher productivity coefficients, higher gross production to biomass ratios, higher net community productivities, lower total biomass, simpler food chains, lower proportions of animals to plants, and r selection pressures. Their radiation utilization efficiencies via gross production are presumably also relatively low. "Immature" communities therefore bear a relationship to "mature" communities resembling the relationship between "spring" and "summer" communities, although the season-specific communities should span a smaller range of productivity ratios and efficiencies than do the seral stages.

As communities and ecosystems evolved through geological time, they probably underwent many of the changes that communities presently undergo during ecological succession. I expect that evolutionarily "primitive" communities had most of the thermodynamic and selection attributes by which Odum (1969) characterized early succession communities, while evolutionarily "advanced" communities have the same characters as Odum's late succession communities (i.e. are synonymous). One possible primitive community may have consisted of an autotroph level and a decomposer level only, each comprised only of micro-organisms. Successive adaptive radiations of increasing complex plants and animals added to community complexity, increased K selection pressures, and progressively shifted community thermodynamic characteristics towards those of present climax communities. Stated explicitly, the surprising conclusion is that primitive communities, because they were dominated by r selected organisms, in many ways utilized energy more efficiently than do modern communities. The latter have advanced primarily in efficiency of radiation utilization via gross production, and in amount of gross production (cf. Section 9.6).

9.8 Efficiency of Energy Utilization by Arctic Communities

I had expected to establish on arriving at this section that the arctic communities I am considering are relatively efficient in terms of their productivity coefficients, even though they are undoubtedly relatively inefficient in their utilization of incoming radiation (e.g. Bliss, 1977b). I expected relatively high community productivity coefficients for two reasons. Firstly, the "climax" communities in these arctic environments appear to varying degrees to be comprised of "early" successional seres. The climatically harsh and disrupting physical environment (e.g. frost heaving) presumably permits continued exploitation by the relatively opportunistic species of earlier successional seres (e.g. Emlen, 1973). As I noted in Section 9.7, "early" (or "immature") communities are distinguished from mature communities by r selection pressures, and therefore by higher productivity coefficients, higher gross production to biomass ratios, higher net community productivities, lower total biomass, simpler food chains, and lower proportions of animals to plants.

The second reason I expected high productivity coefficients in High Arctic communities was by analogy with hot semi-deserts. Hot semi-deserts are evidently dominated by r selected organisms, and fit the general criteria of "early" communities, as evinced by the productivity coefficient of 7.00 (Larcher, 1975). Temperature differences aside, I assumed that hot and cold semi-deserts present very similar problems to the organisms living in them. However, the few production data available for High Arctic communities tell a different and more complex story. Larcher (op. cit.) cited production information for tundra plant communities from which I calculated a productivity coefficient of 3.00. Bliss (1977b) provided similar information for the hummocky sedge-moss meadow, and cushion plant communities (i.e. Polar Semi-desert), from which I calculated productivity coefficients of 1.09 and 1.10 respectively. These coefficients are even lower than that of tropical rain forests at 1.49.

Knowledge of the physiology of the dominant plants, Dryas integrifolia and Carex stans, in these High Arctic communities goes a long way to explaining their low community productivity coefficients. Dryas integrifolia, the dominant woody vascular plant in the cushion plant communities, is a slow growing, long-lived plant (20-120 years) with low productivity (Bliss, 1977a). Most of its biomass (i.e. 62.5-71.4%) is above-ground in its shoots. However, the chlorophyll content of the green tissue is very low, only about 18% of that of Carex stans on a unit weight basis (the rates of photosynthesis per unit weight of chlorophyll are interchangeable between the two species cf. Bliss, 1977b). I conclude that because of the surface habit of this plant, and its location on relatively high, exposed terrain (where it is subject to abrasion by wind-driven ice, etc.) survival requires the development of tough protective non-photosynthetic tissue. Hence, it has a low chlorophyll content, low productivity, and long life.

Carex stans superficially follows a very different strategy. It lives in a more sheltered and wetter environment, and is both shorter-lived (5-7 years) and more productive on a unit weight basis. Moreover, a very large proportion of its production goes into below-ground tissue (i.e. 90.0-92.9% - Bliss, 1977b). However, like *D. integrifolia*, *C. stans* clearly has a very high proportion of respiring but non-photosynthesizing tissue.

In terms of their morphological and physiological strategies for prolonged individual life, I consider both species to be "K" strategists (because these species apparently exhibit only some elements of conventional K strategy, I do not believe that they should be considered typical K strategists). They have achieved this strategy despite their small size relative to more conventional K strategists (e.g. large trees). Evidently low temperatures, in particular, make swift growth and reproduction impractical, so that extended survival of the individual is of paramount concern. This situation contrasts with that in hot semi-deserts, where high temperatures permit rapid growth and reproduction in response to the short wet periods.

Whether or not *Dryas integrifolia* and *Carex stans* also possess the conventional K strategy of superior competitive ability is another matter. They may be competitively superior to lower plants such as the lichens and bryophytes. However, it is almost a contradiction in terms to suggest that competition is a major factor within High Arctic communities. I suspect that these two species are probably competitively inferior in more temperate environments that permit a greater variety of higher plants to survive. It appears to me that *D. integrifolia* and *C. stans* present examples of "K" selection in response to physical conditions, rather than to competitive pressures. If so, conventional theory, with its r and K selection pressures, together with their respective consequences, does not account for organisms such as these, and therefore needs to be expanded accordingly.

In contrast with the autotroph level, the heterotroph levels of these High Arctic communities are dominated by relatively r selected organisms. For example, vertebrate herbivores and predators play a proportionately much smaller role in these communities than they do in many other systems (Bliss, 1977b). This is particularly true of the Polar desert. Furthermore, large above-ground invertebrate herbivores and predators are also relatively unimportant (Ryan, 1977a). On the other hand, Bacteria, Protozoa and the smaller soil-living metazoa such as the Nematoda, Enchytraeidae and Collembola, may occur in densities comparable with those found in many more temperate communities. In contrast with plants, it is apparently more difficult for K selected animals to live permanently in High Arctic communities than it is for r selected animals.

Because the heterotroph component of High Arctic communities is dominated by relatively r selected animals, this component of the community should have a very high productivity coefficient, compared with both the autotroph level, and compared with the heterotroph components of other communities. This is not of course to claim that the proportion of energy passed from autotrophs to heterotrophs is high. Because r selected organisms are, by definition, not food limited, the proportion of energy transfered is likely to be very low. But this need not obscure the likelihood of high efficiency of energy utilization once that energy reaches the High Arctic heterotroph level.

Assuming that my suppositions are correct, High Arctic communities present several anomalies in terms of modern ecological theory. Firstly, the vegetative component of these communities, although having the structural form of "immature" climax, in physiological performance is very much more akin to climax vegetation. In other words, the productivity coefficients and gross production to biomass ratios are very low, as is to be expected of climax vegetation. However, total biomass is also very low, which is not characteristic of climax vegetation. Furthermore, because the heterotroph component of these communities is dominated by r selected organisms, the "climax" vegetation is backed by uncharacteristically low net community productivities (e.g. 0.4-0.5% - Bliss, 1977b), simple food chains, low proportions of animals to plants, and r selection. In other words, the High Arctic community presents a novel juxtaposition of "K" and r selection strategies that confounded my conventional expectations.

To conclude this section I wish to comment upon the stability, and ability to recover from perturbations, of Arctic communities in light of my conclusions regarding the roles of r and K selection in these communities. Bliss (1977b) observed that High Arctic systems like that of Truelove Lowland appear quite stable, and also quite resiliant to severe natural perturbations. He also noted that some biological components are able to respond rapidly to favorable climatic conditions.

Communities comprised of predominantly K selected organisms probably have relatively high resistance to perturbations (i.e. are relatively "buffered"), but have relatively little capacity to recover from such perturbations once they have occurred. For example, the climax plants of tropical rain forests, once removed, are unlikely to re-establish themselves in the face of the changed physical environment and competition encountered by their seedlings. On the other hand, communities in which r selected organisms predominate are relatively well-equipped to recover from major perturbations, if only because their constituent species can build up their populations rapidly in favorable conditions.

The "mixed" nature of some arctic communities means that simple characterization is not possible. On the one hand, some of the dominant plants are relatively "K" selected, and are fairly well buffered against physical perturbations but, once removed, will not return quickly (e.g. particularly *Dryas integrifolia* and lichens). I expect the dominant autotrophs of these communities to be inferior in resiliance to those say, of grasslands, but superior to those of tropical rain forests. On the other hand, the heterotrophic component of these arctic communities, being dominated by relatively r selected micro-organisms and invertebrates, are relatively poorly buffered against perturbations, but compensate with very high resiliance.

I conclude that it is relatively easy to damage the autotrophic component of high arctic communities, but relatively difficult to damage the heterotrophic component (of course, the response of the heterotrophs is affected by that of the autotrophs). I would reverse these conclusions in the case of a subtropical grassland, in which K selected mammals are an important part of the community.

9.9 "What is an Arctic Invertebrate?"

The physiological and ecological characteristics of High Arctic invertebrates in general are poorly known. Most of the relevant knowledge has been gained from the study of the Insecta, as is attested to by the reviews of Downes (1962, 1964, 1965), Oliver (1963, 1968), and MacLean (1975). The pertinent attributes of the Nematoda that fit them for life at these latitudes are particularly poorly known, which is an important oversight in view of their great diversity, and the overwhelming contribution these animals make to energy flow through High Arctic invertebrate faunas.

Perhaps the general quality that most contributes to the success of nematodes in high latitudes is their low level of specialization, which permits them to occupy a wide range of niches. Whether their niches are defined in terms of the food resources exploited, reproductive capability, or physiological tolerance, free-living soil nematodes are impressive in their flexibility.

I documented the striking flexibility of some species of nematodes in the range of food they exploit in Chapter 2.3.2.5. Kauri (1975) noted that there is a multitude of food resources even in the tundra (for birds), but also observed that most of the resource "packages" lie beneath or near the threshold level and/or fluctuate, and provide insufficient basis for specialization. Generalist nematodes derived from more temperate faunas are therefore preadapted nutritionally to exploit the resource situation in High Arctic communities. At the same time, the High Arctic resource situation does not favour the evolution of endemic "specialist" species, nor the development of "generalist" species from low latitude specialists.

A corollary of the generalist capabilities of High Arctic nematodes (and, presumably, other High Arctic invertebrates) is the difficulty in assigning them specific trophic roles. This confounds the expectation that energy pathways are more easily defined and quantified in "simple" high latitude communities than they are in "complex" low latitude communities dominated by specialists.

The advantages of flexibility in fitting organisms for life in high latitudes is also demonstrated by the nature of nematode reproduction. Although most species of soil and plant nematodes are bisexual, in many species, including _Chiloplacus_ sp., males are rare, and reproduction is by parthenogenesis (alternatively, some species are hermaphroditic, and reproduce by automixis - Triantaphyllou, 1971). Yeates (1970b) noted that parthenogenesis (and hermaphroditism) better fits these animals for colonizing new localities than does obligate bisexual reproduction, because only one reproductive individual is required to start a population. Parthenogenesis is also a superb attribute for exploiting low amounts of resource that are highly dispersed (e.g. plants in Polar Desert communities). In High Arctic communities resources (e.g. plants) may be too dispersed to support populations of obligate sexually reproducing species, which must maintain a minimum density to permit the sexes to meet. The same resources however, may support parthenogenic species which have no minimum density restrictions (such species may also be very difficult to detect!).

Nematodes provide several examples of environmentally controlled sex expression (e.g. Triantaphyllou, 1971). Low temperature has been shown to increase the proportion of females in some species (e.g. Aphelenchus avenae - Dao, 1970). Spaull (1973b) has suggested that such a mechanism is important in establishing nematodes in cold regions.

Parthenogenic (and hermaphroditic) reproduction can lead to polyploidy - which may also aid life in high latitudes. Schmalhausen (1960) suggested that the diploidy of an organism is a general means of protection against the disturbing effect of "noise". He suggests that the "noise - resistance" of polyploids, which are often found in plants living under the harsh climatic conditions of mountains and the Arctic (e.g. Löve and Löve, 1975), is even higher.

Löve and Löve (op. cit.) stated that polyploidy (in plants) affects dispersal and survival by increasing considerably the adaptability of the of the species to all kinds of extreme stress. Polyploidy has been shown to occur in nematodes (e.g. the Heterodera - Triantaphyllou, 1971) and may prove to be a factor in their success in these extreme environments.

Spaull (1973b) presented evidence that indicates unisexual nematode species have a greater chance of establishing themselves in new cold localities than do bisexual species. He found that on sub-Antarctic Signy Island (60°43'S) males were rare or absent in less than 50% of the genera, whereas on Alamonde Island (68°43'S) the proportion was approximately 75%.

Members of other important invertebrate groups in the High Arctic also exhibit parthenogenesis or hermaphroditism. For example, species of Collembola belonging to the genera Onychiurus (Rapoport and Aguirre, 1973), Tullbergia and Isotoma (Petersen, 1971) exhibit parthenogenesis, as do the Acarina (e.g. Grandjean, 1941) and Chironomidae (Grodhaus, 1971; Lindeberg, 1971). The Enchytraeidae exhibit both parthenogenesis and polyploidy (e.g. Christensen, 1961).

Nematodes possess an important co-requisite for successful reproduction in the High Arctic, namely the ability to extend individual life beyond one growing season. A single growing season is usually too cold and short to permit most invertebrates to complete their life cycles in one year. For similar reasons, arctic plants are mostly perennials, rather than annuals (e.g. Löve and Löve, 1975).

As generally r selected organisms, High Arctic nematodes and other invertebrates also exhibit relatively early reproduction, single reproduction, many small offspring, and high maximal rate of increase, r_{max}, insofar as low temperatures and dry conditions permit expression of these qualities.

As a negative consequence of r selection, High Arctic invertebrates should have inferior interspecific competitive abilities in relatively "saturated" communities (i.e. in more temperate environments).

Physiological attributes should include raised metabolic rates at low temperatures (which will be most evident in endemic species); regions of thermoneutrality in the metabolic curves corresponding to the commonly encountered environmental temperatures; capacity for "freezing resistance" or "freezing tolerance" (e.g. Asahina, 1969); small size (and favourable surface-volume ratios) in order to avoid exposure and to best utilize favourable microclimates; and, as r selected organisms, high individual and population production and productivity coefficients.

Finally, these animals should have superior dispersal capabilities which, however, may be either active or passive.

In view of the overwhelming importance I have established for nematodes in High Arctic communities, I feel that the best answer to Downes' modified question - "What is an Arctic Invertebrate?" - is not to be obtained by applying to the group as a whole. Insofar as any one invertebrate group can do so, the free-living soil nematodes embody those attributes necessary for invertebrate life in High Arctic regions. Therefore my answer to - "What is an Arctic Invertebrate?" - is: - "It is an Arctic Nematode!"

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VITA

I was born on 17 January 1945, in Christchurch, New Zealand. I began school at Christchurch, but I obtained virtually all of my primary education at Karitane, which is a small fishing village in the province of Otago. The first two years of my secondary education were at Horowhenua College, Levin, in New Zealand, and my final three years were at Riccarton High School, back in Christchurch.

Following high school, I attended the University of Canturbury at Christchurch, from which I graduated B.Sc. Hons. in Zoology. In addition to the bursaries I received, I supported myself by working in a local sawmill. My parents also helped, particularly during my final year, prior to which I had hitch-hiked around Australia, and from which trip I had arrived home penniless.

Immediately upon graduation I went to the Antarctic as a research scientist with the University of Canterbury Antarctic Biology Unit. I published my first paper out of this experience. On returning from the Antarctic I obtained the position of science teacher at Darfield High School, 40 miles from Christchurch, where I remained for 8 months.

My spell of teaching at Darfield High School filled in my time prior to leaving for the University of British Columbia, Canada, which I attended as a graduate student in Zoology. In order to save money on the trip across the Pacific Ocean, I hitch-hiked via cargo ship to the eastern seaboard of the United States, from where I bused to British Columbia. At U.B.C. I participated in an I.B.P. study of a small lake, and obtained an M.Sc. for my contributions. During this period I was supported by graduate teaching and research assistantships, and also a scholarship. During my last year at U.B.C. I was also employed by the International Pacific Salmon Fisheries Commission, Cultus Lake, as a research scientist.

Following graduation from the University of British Columbia, I went to the University of Alberta, where I have been enrolled as a graduate student in Entomology to the present time. There I performed the research described in this thesis. The university supported me with graduate teaching assisstantships and intersession bursaries, while the Devon Island I.B.P. Project provided research assistantships.

I am presently a member of the staff of the Department of Biology, University College of Botswana, where I am teaching undergraduate entomology, ecology and applied biology, as well as conducting my own research. I am filling this position as part of Canada's foreign aid program to developing countries and, as such, I am under contract to the Canadian International Development Agency and the World University Service of Canada.